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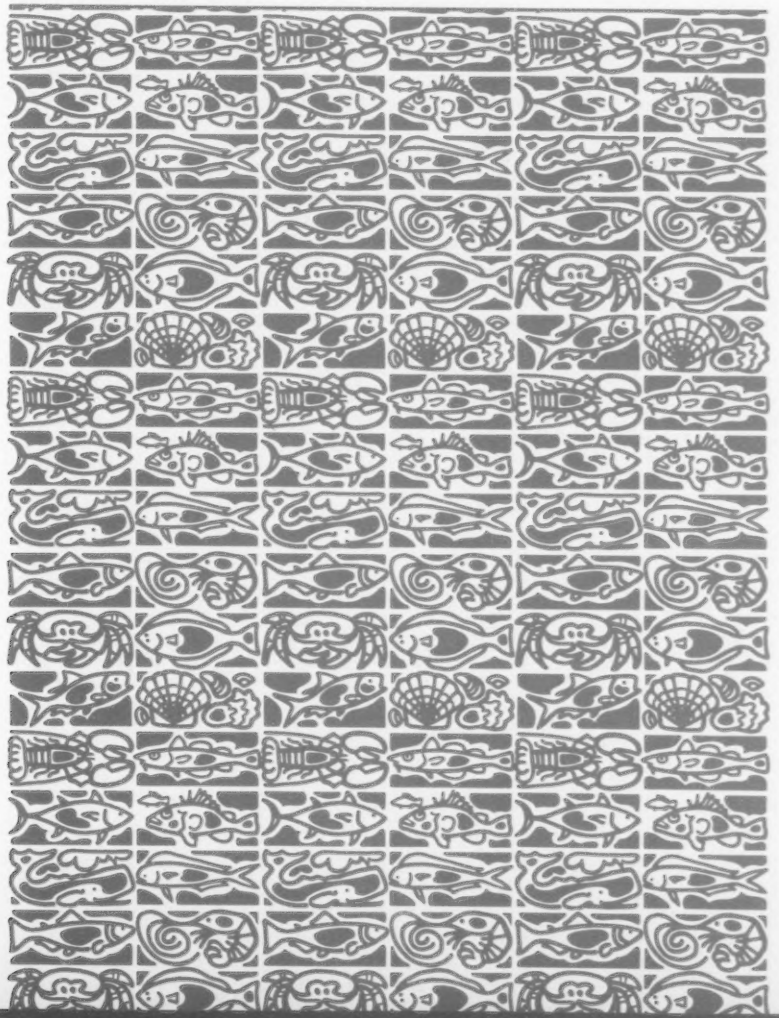

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Fishery Bulletin

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Editorial Assistant
Sarah Shoffler

Southeast Fisheries Science Center
National Marine Fisheries Service, NOAA
101 Pivers Island Road
Beaufort, NC 28516

Managing Editor
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National Marine Fisheries Service
Scientific Publications Office
7600 Sand Point Way NE, BIN C15700
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Variation in life history parameters of Dover sole, *Microstomus pacificus*, off the coasts of Washington, Oregon, and northern California

Jon Brodziak
Hatfield Marine Science Center
Northwest Fisheries Science Center
National Marine Fisheries Service, NOAA
2030 SE Marine Science Drive
Newport, Oregon 97365
Present address: Northeast Fisheries Science Center
166 Water Street
Woods Hole, Massachusetts 02543
E-mail address: Jon.Brodziak@noaa.gov

Robert Mikus
Hatfield Marine Science Center
Oregon Department of Fish and Wildlife
2040 SE Marine Science Drive
Newport, Oregon 97365

Abstract–Variation in the life history parameters of Dover sole (*Microstomus pacificus*) off the coasts of Washington, Oregon, and northern California was investigated by using research survey data. We compared growth, maturation, and length-weight curves of Dover sole within the International North Pacific Fisheries Commission (INPFC) statistical areas of Monterey, Eureka, Columbia, and Vancouver. We found strong evidence of dimorphism in growth and maturation rates between sexes. In addition, geographic variation in both growth and maturation rates was also suggested. Male and female Dover sole from the Columbia area had lower Brody growth coefficients and larger asymptotic lengths than Dover sole from other areas. Further, there was an apparent latitudinal cline in maturation rates because males and females matured at smaller size and younger ages at higher latitudes. In contrast, no difference between male and female length-weight relationships was detected. In comparison with other pleuronectids, we found that Dover sole matured at relatively larger sizes and younger ages. These differences likely reflect adaptation of Dover sole to the inherent variability of the California Current.

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Dover sole (*Microstomus pacificus*) is a deep-water pleuronectid fish that ranges from Baja, California, to the Bering Sea (Hart, 1973) at depths from 10 m to 1200 m (Pearcy et al., 1982; Allen and Smith, 1988). Dover sole are demersal and have a complex life history that includes an extended pelagic larval phase of one year or more (Pearcy et al., 1977; Markle et al., 1992; Toole et al., 1993; Butler et al., 1996) and an ontogenetic migration range from continental shelf to continental slope (Jacobson and Hunter, 1993). Dover sole support an important commercial fishery off the coasts of Washington, Oregon, and California, where annual landings have averaged about 12,000 t during 1956–96 (Brodziak et al., 1997).

Previous research on life history parameters of Dover sole off the west coast of the United States was conducted during the late 1940s and the 1980s. Hagerman (1952) estimated growth, maturation rates, and length-weight curves of Dover sole from commercial fishery samples collected from the ports of Eureka and Fort Bragg, California during 1948–49. Harry (1959) estimated maturation rates of Dover sole from commercial fishery samples collected at the port of Astoria, Oregon, during 1948–49. More recently, Hunter et al. (1990) have estimated growth and maturation rates of Dover sole from research survey samples collected between Point Conception and Half Moon Bay, California, during 1985–88. Hunter et al. (1992) refined maturation rate estimates of female Dover sole through histological analysis of survey data collected off the coasts of Oregon and California during 1985–89.

In this study, we investigated variation in life history parameters of Dover sole off the coasts of Washington, Oregon, and northern California from samples collected during research surveys during 1984–85 and 1990–93. Dover sole samples were partitioned into geographic regions based on International North Pacific Fisheries Commission statistical areas in order to investigate latitudinal differences among potential management units. We used length-at-age data to estimate growth and to quantify sexual dimorphism and geographic variation in growth. Maturation of male and female Dover sole as a function of length and age was estimated and geographic variation in maturity was quantified. Sexual dimorphism and geographic variation on weight at length were also explored. We discuss apparent differences between life history parameters of Dover sole and other pleuronectids.

Materials and methods

Length-at-age samples

A total of 4780 Dover sole were collected for age determination during 1984–93 from bottom trawl surveys of the upper continental slope (Raymore and Weinberg, 1990; Parks et al., 1993; Lauth et al., 1997). Biological samples were collected from three depth strata (183–549 m, 550–914 m, and 915–1280 m) within the International North Pacific Fisheries Commission (INPFC) statistical areas (Table 1; Fig. 1) of Monterey (38°24′N–40°30′N), Eureka (40°30′N–43°00′N), Columbia (43°00′N–47°30′N), and Vancouver (47°30′N–48°29′33″N). The survey area was length- and depth-stratified to ensure adequate coverage for otolith sampling. For each fish collected, sex was determined, total length (to the nearest cm) was measured, and otoliths were extracted for age determination.

Maturity stage was determined for 4490 Dover sole by visual inspection of gonads. Only samples from surveys conducted by the RV *Miller Freeman* (Table 1) were used for analyzing maturity rates because these samples were collected prior to the spawning season during winter when gross anatomical features provide a reasonably accurate measure for determining whether a fish is mature or not (Hagerman, 1952; Hunter et al., 1992). Total fish weights (to the nearest gram) were also recorded for 3019 samples from surveys conducted by the MV *Half Moon Bay* and the RV *Miller Freeman*; these data were used for length-weight analyses.

Fish ages were determined by the break and burn method, which is the standard for Dover sole (Pikitch and Demory, 1988), although the method has not been validated. In our study, the initial otolith increment was assumed to be an age-1 marker in accordance with the convention for aging adult Dover sole (Chilton and Beamish, 1982). Increments in each otolith were counted two or more times and assigned a single age by one of four readers. In some cases, a mark within the otolith core was counted as the initial increment because it met the identification criteria of an annual increment. A paired comparison of age readings between the most experienced reader and the other readers indicated that there was a mean difference of μ=0.22 years (σ_{μ}=0.13) based on a blind sample of 474 Dover sole; this difference was almost significant at the 5% level (P=0.08).

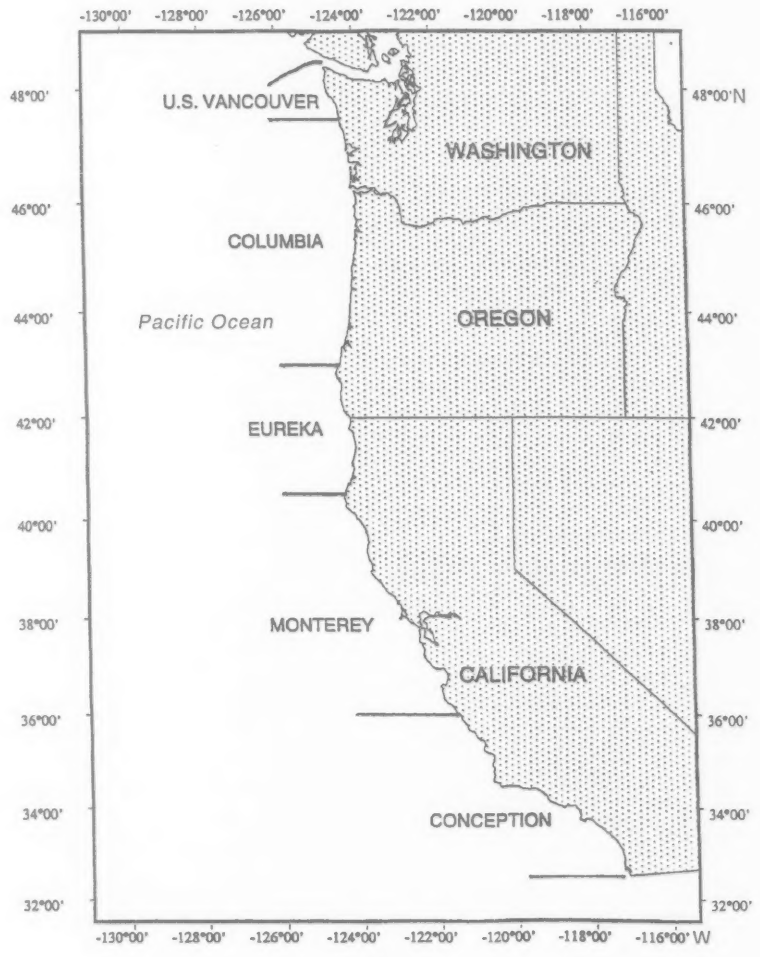

Figure 1

International North Pacific Fisheries Commission statistical areas in the North Pacific Ocean.

Empirical comparisons of mean ages, lengths, and weights by sex within each INPFC area were performed. The GT2 test is appropriate for unplanned comparisons of populations with unequal sample sizes (Sokal and Rohlf, 1981) and it was used to test for differences in mean age, length, and sex among INPFC areas.

Growth curves

Bartlett's test of homogeneity of variance was used to test whether variance in length at age varied by sex for Dover sole from ages 3 to 30 years. Test results were used to select an appropriate error structure for growth curve estimation. Growth curves for male, female, and pooled-sex samples were estimated by maximum likelihood (see Kimura, 1980). We used an alternative parameterization of the von Bertalanffy growth curve (Schnute

Table 1

Dover sole samples used for growth, maturity,[1] and length-weight[2] analyses by INPFC area, vessel, month and year of collection, and depth range of capture.

INPFC area		Number of males	Number of females	Total	Vessel	Month and year	Depth range (m)
Vancouver		94	97	191	FV *Marathon*	Apr 1985	221–406
		41	59	100	FV *Mys. Babushkina*	May 1985	188–280
		77	60	137	RV *Miller Freeman*	Oct 1992	225–854
	Total	212	216	428			
Columbia		329	54	383	FV *Poseydon*	Apr 1984	320–450
		596	331	927	MV *Half Moon Bay*	Sep 1984	110–856
		419	248	667	FV *Marathon*	Apr 1985	188–448
		230	88	318	FV *Mys. Babushkina*	May 1985	115–262
		162	236	398	RV *Miller Freeman*	Oct 1992	210–1211
		182	240	422	RV *Miller Freeman*	Oct 1993	192–1132
	Total	1918	1197	311			
Eureka		226	303	529	RV *Miller Freeman*	Oct 1990	252–1189
		37	39	76	RV *Miller Freeman*	Oct 1991	229–1176
		54	75	129	RV *Miller Freeman*	Oct 1993	243–1163
	Total	317	417	734			
Monterey		209	294	503	RV *Miller Freeman*	Oct 1991	198–1130

[1] Maturity analyses comprised data from surveys conducted by the RV *Miller Freeman*.
[2] Length-weight analyses comprised data from surveys conducted by the RV *Miller Freeman* and the MV *Half Moon Bay*.

and Fournier, 1980; Ratkowsky, 1983) because its parameters were simpler to interpret and because it exhibited better statistical properties than other parameterizations of the von Bertalanffy model. This form was

$$L(t_i) = L_{\min} + (L_{\max} - L_{\min})\frac{(1-c^{t_i - t_{\min}})}{(1-c^{t_{\max} - t_{\min}})} + \varepsilon_i, \qquad (1)$$

where t_i = age of the i^{th} sample;
L_{min}, L_{max}, and c = parameters;
t_{min} and t_{max} denote the youngest and oldest ages observed in the length-at-age sample;
L_{min} and L_{max} denote the predicted lengths at ages t_{min} and t_{max}; and
ε_i = independent and identically distributed normal error terms with zero mean and constant variance $\varepsilon_i \sim N(0, \sigma^2)$.

There is a one-to-one relationship between parameters of the alternative form and the standard von Bertalanffy model (see Ratkowsky, 1983). Residuals from estimated growth models were tested for normality with the Shapiro and Wilk (1965) test. Standard errors of parameter estimates were computed by using the conditional bootstrap with 1000 bootstrap replicates (Efron and Tibshirani, 1993), except for the pooled-sex analysis, where asymptotic standard error estimates were used owing to the large sample size.

As found in previous research, some sexual dimorphism in growth was expected, but there was no information about geographic variation in growth. A likelihood-ratio test (Kimura, 1980) was applied to determine whether growth curves differed by sex or by INPFC area. This test compared two hypotheses: H_0, the hypothesis of identical growth parameters between sexes or among areas; and H_1, the hypothesis of different growth parameters. The test statistic (χ^2) was

$$X^2 = -N \log\left(\frac{\sigma_1^2}{\sigma_0^2}\right), \qquad (2)$$

where σ_0^2 and σ_1^2 = sample estimates of residual variance for growth curves estimated under H_0 and H_1.

The likelihood-ratio test was applied to male and female samples from all INPFC areas and was then separately applied to male and female samples for paired adjacent INPFC areas. When there was no difference between adjacent areas, samples were grouped and the process was repeated. Standard errors of parameter estimates of the final groups were computed by using the conditional bootstrap with 1000 replicates.

Maturation curves

Maturation by length and by age were estimated for female (n=934) and male (n=1232) Dover sole with logistic regression (McCullagh and Nelder, 1989). Significance of fish length or age as a predictor of fraction mature was tested with the likelihood-ratio chi-square test. Standard errors for model parameters were estimated by using the nonparametric bootstrap method with 1000 replicates.

Geographic differences in maturation rates were also evaluated for male and female samples by using logistic regression. Step-wise model selection was used to determine the best model of length or age and the factors INPFC area and sex, and all possible higher order interactions between these terms. The full model with all possible interactions was

$$\log\left(\frac{\pi}{1-\pi}\right) = (\beta_0 + \beta_A + \beta_S + \mathrm{B}_{AS}) + (\beta_1 + \beta_{1A} + \beta_{1S} + \beta_{1AS})X, \quad (3)$$

where π = the probability of being sexually mature;

β_A, β_S, and β_{AS} = coefficients of area, sex, and their interaction; and

β_{1A}, β_{1S}, and β_{1AS} = coefficients of first- and second-order interactions between area, sex, and the variable length (or age), denoted by X.

Akaike's information criterion (AIC) was used to compare competing nested models in a step-wise manner (Hastie and Pregibon, 1993). We also evaluated whether overdispersion due to cluster sampling was present (McCullagh and Nelder, 1989). If the ratio of observed to expected sampling variation (ϕ) for the estimated model was less than 1, we concluded that overdispersion was not present. Nonparametric bootstrapping based on 1000 replicates was used to estimate standard errors for parameter estimates.

Length-weight curves

We estimated length-weight relationships for pooled-sex, male (n=1549), and female (n=1470) samples based on the allometric equation

$$W_i = AL_i^B \exp(\varepsilon_i), \quad (4)$$

where W_i and L_i = the observed total weight (grams) and total length (centimeters) of the i^{th} fish;

A and B = parameters; and

ε_i = independent and identically distributed normal error terms with zero mean and constant variance.

A natural logarithmic transformation was applied to length and weight measurements and linear regression was applied to estimate parameters, denoted as b_0=log$A$ and b_1=B. Because lognormal errors were assumed, the retransformed intercept needs to be adjusted to give an accurate predictive equation for mean weight, and the adjusted intercept was computed as A=exp(b_0)exp((σ^2– $\sigma_0{}^2$)/2), where σ^2 is the residual variance from the regression and $\sigma_0{}^2$ is the variance of b_0 (Hayes et al., 1995). Nonparametric bootstrapping with 1000 replicates was used to estimate standard errors of parameters and to provide nominal estimates of parameter bias (Efron and Tibshirani, 1993).

Geographic variation and sexual dimorphism in the length-weight relationship for Dover sole were investigated by a step-wise procedure among generalized linear models relating the log-transformed length-weight observations to the factors INPFC area and sex, and all possible higher order interactions between these terms. The full model with all possible interactions was

$$\log W_i = (\log A + \beta_A + \beta_S + \beta_{AS}) + (B + \beta_{AL} + \beta_{SL} + \beta_{ASL}) \log L_i + \varepsilon_i, \quad (5)$$

where β, β_S, and β_{AS} = coefficients of area, sex, and their interaction;

β_{AL}, β_{SL}, and β_{ASL} = coefficients of first- and second-order interactions between area, sex, and the natural logarithm of length; and

ε_i = a normally distributed error with zero mean and constant variance.

As in the maturity analyses, the AIC criterion was used to choose among competing models in a step-wise manner (Hastie and Pregibon, 1993). Estimates of standard errors of parameters and nominal estimates of parameter bias were computed with the nonparametric bootstrap with 1000 replicates. Bootstrap estimates of residual variance and $\sigma_0{}^2$ = Var[b_0]=Var[log$A$+β_A+β_S+β_{AS}] were used to compute the adjusted intercept.

Results

Length-at-age samples

Female and male age and total length distributions differed across areas. On average, females were 1 to 2 years older than males (Table 2). Mean ages of males and females were significantly different for all areas combined and within the Vancouver, Columbia, and Eureka areas (P<0.05). Mean ages were lowest in the Vancouver area and highest in the Eureka area. The youngest males were 2 years old and had lengths of 19, 22, and 25 cm, whereas the oldest male was 42 years old and 41 cm long. The youngest female was 2 years old and 21 cm long, whereas the oldest female was 48 years old and 51 cm long. Maximum observed ages of females were greater than those of males in all areas except the Vancouver area where the fewest samples were collected. Females were 4 to 5 cm longer than males on average (Table 2). Mean female

Table 2

Dover sole mean, minimum (Min), and maximum (Max) ages (yr), total lengths (cm), and total weights (g) by INPFC area and sex. Standard errors (SE) of mean values appear in parentheses.

		Age (yr)			Length (cm)			Weight (g)		
INPFC area	Sex	Min	Mean (SE)	Max	Min	Mean (SE)	Max	Min	Mean (SE)	Max
Vancouver	Male	3	10.2 (0.3)	39	20	33.1 (0.4)	49	97	505 (32)	1195
	Female	4	11.1 (0.3)	29	21	37.4 (0.5)	57	114	704 (55)	1850
Columbia	Male	3	11.9 (0.1)	42	17	33.6 (0.1)	51	40	467 (9)	1325
	Female	3	14.0 (0.2)	48	15	38.8 (0.2)	66	33	660 (14)	2479
Eureka	Male	2	13.0 (0.4)	35	16	35.4 (0.4)	49	48	485 (15)	1182
	Female	3	14.5 (0.4)	40	21	40.6 (0.4)	56	75	789 (23)	2296
Monterey	Male	3	12.7 (0.5)	31	19	35.4 (0.5)	49	55	499 (19)	1240
	Female	2	13.6 (0.4)	42	20	39.4 (0.5)	55	65	741 (27)	2157
All areas	Male	2	12.0 (0.1)	42	16	33.9 (0.1)	51	40	478 (7)	1325
	Female	2	13.7 (0.1)	48	15	39.1 (0.2)	66	33	712 (11)	2479
	Pooled	2	12.7 (0.1)	48	15	36.2 (0.1)	66	33	598 (7)	2479

length was significantly greater than mean male length for all areas combined and within each area ($P<0.05$). Mean lengths were greatest within the Eureka and Monterey areas and smallest in the Vancouver area. The smallest male (16 cm) was 4 years old, whereas the two largest males (51 cm) were 25 and 37 years old. The smallest female (15 cm) was 2 years old and the largest female (66 cm) was 38 years old.

Weight distributions differed by sex across areas. Mean female weights exceeded male values by 200 to 300 g. Significant differences between male and female weight were detected for all areas combined and within each area ($P<0.05$). Individual fish weights were more variable for females than for males. Mean weights were greatest within the Eureka and Monterey areas and lowest in the Columbia area. The lightest male weighed 40 g and was 5 years old, whereas the heaviest male was 1325 g and 26 years old. The lightest female weighed 33 g and was 5 years old, whereas the heaviest female was 2479 g and 38 years old.

Growth curves

Variances in length at age of male and female Dover sole were homogeneous. For male samples (n=2613), the coefficient of variation (CV) of length at age ranged from 6 to 14% and averaged 10%, with an average variance of 12.5 cm. Male variance in length was homogeneous across ages (P=0.83, χ^2=20.97). For female samples (n=2514), the CV ranged from 6 to 16% and averaged 11%, with an average variance of 17.5 cm. Similar to that for males, female variance in length was homogeneous across ages (P=0.59, χ^2=25.64). As a result, we used an additive normal error term for estimating growth curves.

There was sexual dimorphism in growth of Dover sole when samples were pooled across areas. Maximum likelihood estimates and standard errors (SE) for pooled-sex samples were as follows: L_{max} = 51.3 cm, SE = 0.5; L_{min} = 20.9 cm, SE = 0.3; c = 0.9337, SE = 0.0030 with corresponding von Bertalanffy values: L_∞ = 52.6 cm, K = 0.069, and t_0 = −5.4. Male and female growth parameters for all areas (Table 3) were significantly different ($P<0.001$, χ^2=1079) and showed that females grow more rapidly than males and attain larger sizes. There was greater variation in female size at age, and residual variance from the female curve was roughly twice that value from the male curve. Both female and male curves for samples pooled across areas did not satisfy the assumption of normally distributed residuals ($P<0.01$). Thus, neither male nor female growth was adequately described by a single growth curve representing all areas.

Geographic variation was evident in male growth curves estimated for each area (Table 3). The hypothesis of identical growth parameters for all areas was rejected ($P<0.001$, χ^2=96.25). Male samples from adjacent INPFC areas were grouped and growth curves were estimated. Homogeneous growth was rejected for Vancouver and Columbia samples ($P<0.001$, χ^2=25.88) and for Columbia and Eureka samples ($P<0.001$, χ^2=42.31) but was accepted for the Eureka and Monterey samples (P=0.28, χ^2=3.85). Homogeneous growth was rejected for combined samples from Eureka, Monterey, and Columbia ($P<0.001$, χ^2=80.98) but was accepted for combined male samples from Eureka, Monterey, and Vancouver (P=0.35, χ^2=6.65).

We found that growth of male Dover sole differed between the Columbia area and the combined Vancouver, Eureka, and Monterey areas (Table 3) and that male growth curves from the Vancouver, Eureka, and Monterey

areas were not statistically distinguishable. Males from the Columbia area grew more slowly and reached larger sizes, on average, than males from the Vancouver, Eureka, and Monterey areas (Fig. 2A). Estimates of L_∞ and K for the Columbia area differed from estimates for the combined Vancouver, Eureka, and Monterey areas by 3% and –26%, respectively. Parameters of the alternative growth curve were more precisely determined with CVs of 1–3% for the Columbia and combined areas in comparison to the standard von Bertalanffy model where CVs were 2–14%. Residual variance for the Columbia area was lower than that for the three areas combined. However, residuals from the Columbia area curve did not satisfy the normality assumption (P=0.01), whereas residuals from the combined areas did (P=0.83). Overall, there was no latitudinal cline in growth parameters.

Similarly, we found geographic variation in growth of female Dover sole by area (Table 3). The hypothesis of identical female growth parameters across areas was rejected (P<0.001, χ^2=91.70). Female samples from adjacent INPFC areas were grouped and growth curves were estimated. Homogeneous growth was rejected for Vancouver and Columbia samples (P=0.002, χ^2=14.92) and for Columbia and Eureka samples (P<0.001, c=56.90) but was accepted for Eureka and Monterey samples (P=0.09, χ^2=6.45). Homogeneous growth was rejected for combined samples from Eureka, Monterey, and Columbia (P<0.001, χ^2=89.15) and weakly supported for combined samples from Eureka, Monterey, and Vancouver (P=0.025, χ^2=14.47).

Growth of female Dover sole exhibited geographic variation (Fig. 2B). In particular, females from the Columbia

Table 3

Estimated growth curves for length (cm) at age (yr) of male and female Dover sole by INPFC area. Parameters L_{max} L_{min} and c are from the empirical von Bertalanffy curve. Corresponding values for the standard von Bertalanffy curve (L_∞, t_0, and K) are also listed. Bootstrap estimates of standard errors appear immediately below each estimate in parentheses. Other table entries are the residual variance from the nonlinear regression (σ^2) and the probability that residuals were normally distributed (P(normal)) based on the Shapiro and Wilk (1965) test.

Growth curves by INPFC area	L_{max}	L_{min}	c	σ^2	P(normal)	L_∞	t_0	K
Male growth curves								
All areas[1]	46.6	21.2	0.9315	11.45	<0.01	48.2	–6.2	0.071
	(0.5)	(0.4)	(0.0042)			(0.8)	(0.5)	(0.005)
Vancouver	45.9	21.8	0.9102	13.03	0.51	47.8	–3.7	0.094
	(1.6)	(1.0)	(0.0157)			(2.3)	(1.3)	(0.017)
Columbia	46.4	23.0	0.9347	10.92	0.01	48.2	–6.6	0.068
	(0.6)	(0.4)	(0.0053)			(1.1)	(0.7)	(0.006)
Eureka	45.7	20.8	0.9182	11.37	0.71	47.3	–4.8	0.085
	(0.9)	(0.8)	(0.0102)			(1.5)	(0.9)	(0.011)
Monterey	43.7	22.6	0.8910	10.21	0.95	44.6	–3.1	0.115
	(0.8)	(0.8)	(0.0146)			(1.2)	(0.9)	(0.016)
Vancouver, Eureka,	45.7	20.4	0.9121	11.53	0.83	46.6	–4.3	0.092
and Monterey	(0.7)	(0.6)	(0.0072)			(0.9)	(0.6)	(0.008)
Female growth curves								
All areas	51.7	19.7	0.9131	20.06	<0.01	52.2	–3.2	0.091
	(0.5)	(0.6)	(0.0042)			(0.6)	(0.4)	(0.005)
Vancouver	51.0	24.5	0.9135	24.18	0.87	54.1	–2.7	0.091
	(1.9)	(1.5)	(0.0219)			(5.1)	(1.7)	(0.024)
Columbia	51.8	22.5	0.9206	19.93	0.63	52.5	–3.8	0.083
	(0.7)	(0.7)	(0.0057)			(0.9)	(0.6)	(0.006)
Eureka	50.8	20.8	0.8879	17.94	0.24	51.1	–1.4	0.119
	(0.7)	(1.0)	(0.0091)			(0.8)	(0.6)	(0.010)
Monterey	49.7	19.1	0.8849	15.03	0.99	49.9	–1.9	0.122
	(0.8)	(1.1)	(0.0103)			(0.9)	(0.6)	(0.012)
Vancouver, Eureka,	51.0	18.5	0.8965	18.64	0.58	51.4	–2.1	0.109
and Monterey	(0.8)	(0.8)	(0.0060)			(0.7)	(0.4)	(0.007)

[1] INPFC areas sampled in the study: Vancouver, Columbia, Eureka, and Monterey.

area appeared to grow more slowly and achieve greater sizes than females from the other areas. Estimates of female L_∞ and K from the Columbia area were 2% and –24% different from estimates for the combined Vancouver, Eureka, and Monterey areas (Table 3). As with the results for males, female growth parameters were more precisely estimated for the alternative growth curve with CVs of 1–6% in comparison with CVs of 2–65% for the standard von Bertalanffy curve. In contrast to males, residuals of female growth curves were normally distributed and there was an apparent increase in L_∞ with latitude. Overall, geographic variation of male and female growth was similar, with the exception that asymptotic female size appeared to increase with latitude.

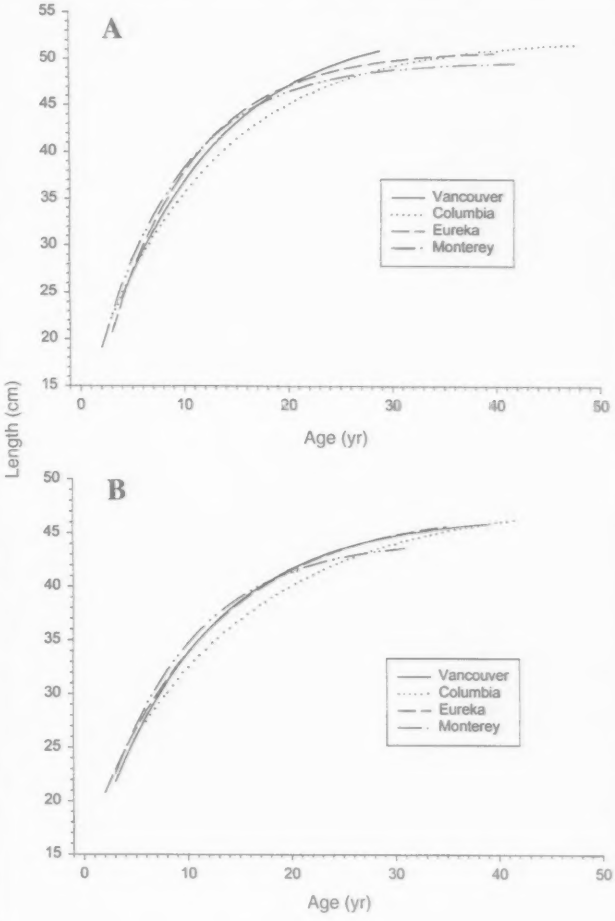

Figure 2

Dover sole growth curves (total length on age) by INPFC area for females (**A**) and for males (**B**).

Maturation curves

We found that male Dover sole matured at smaller sizes than did females when samples were combined across areas (Table 4). Predicted female median length at maturity (L_{50}) exceeded male L_{50} by 6 cm (23%), and the ratio of median length at maturity to asymptotic size (L_{50}/L_∞) of females exceeded that of males by 14%. The estimate of male L_{50} (CV=2%) was more variable than the female L_{50} (CV=1%).

Maturity-at-age curves for all areas (Table 5) indicated that males matured at younger ages than females. Predicted female median age at maturity (A_{50}) exceeded male A_{50} by three years (57%), whereas the ratio of female median age at maturity to maximum observed age (A_{50}/A_{max}) exceeded that of males by about 42%. The estimate of male A_{50} (CV=10%) was less precise than the female estimate (CV=3%).

Geographic variation was evident in maturity at length by INPFC area (Fig. 3). The best logistic model for maturity at length included terms[1] for length, sex, area, length×sex, and length×area and had a dispersion parameter of ϕ = 1.28 (Table 4). This factor indicated a moderate degree of overdispersion in the maturity-at-length data. Male maturity curves by INPFC area showed a geographic cline in L_{50}, and median size at maturity decreased with latitude. Male L_{50} values ranged from 22 to 29 cm with CVs of 2% to 9%. Similarly, the ratio L_{50}/L_∞ decreased from 0.66 in Monterey to 0.47 in Vancouver. Female L_{50}'s showed a similar geographic cline, although female L_{50}'s were more precisely estimated than male L_{50}'s. Female L_{50} values ranged from 35 cm in Monterey to 28 cm in Vancouver. Female values of L_{50}/L_∞ also decreased as latitude increased. Overall, median length at maturity of both male and female Dover sole decreased with increasing latitude.

Maturity at age also varied by INPFC area (Fig. 4). The best logistic model included terms for age, sex, area, age×sex, and age×area (Table 5). Dover sole maturity-at-age data were highly overdispersed and the ratio of observed-to-expected sampling variance for the selected model was ϕ = 4.86. Male maturity ogives by INFPC area suggested a latitudinal cline in A_{50}. Male A_{50} values ranged from 3 to 7 years and decreased with increasing latitude, except for the Columbia area. CVs of male A_{50} values were high and ranged from 8% to 70%. The ratio A_{50}/A_{max} showed a clear latitudinal trend and decreased from 0.22 in Monterey to 0.09 in Vancouver. Female A_{50} values decreased as latitude increased and ranged from 9 years in Monterey to 6 years in Vancouver. Estimates of female A_{50} by INPFC area were more precise than those for males (with CVs of 5–20%). Female ratios of A_{50}/A_{max}

[1] *XY* denotes an interaction between *X* and *Y*.

had no obvious latitudinal pattern and were relatively similar (0.16 to 0.21) across areas. Overall, median age at maturity of both male and female Dover sole appeared to decrease with increasing latitude.

Length-weight curves

Length-weight curves for all areas combined were highly significant ($P<0.001$) for pooled-sex, male, and female samples (Table 6). Males had a larger length exponent than females but there was little apparent difference between male and female curves. For pooled-sex samples, the length exponent exceeded 3 and showed that Dover sole weight in autumn was more than proportional to the cube of length. CVs of intercept parameters ranged from 3% to 5% for pooled-sexes, males, and females, whereas CVs of length exponents were all less than 1%. Bootstrap estimates of parameter bias were low compared with standard errors and were less than 0.3% of point estimate in all cases. For the intercept parameter, ratios of bias to standard error were –1%, 5%, and 6% in pooled-sex, male, and female samples. Corresponding ratios for the length exponent were 2%, –2%, and –4%.

Geographic variation in length-weight relationships of Dover sole was suggested by the generalized linear model analyses. The best model contained the terms for log(*length*), *area*, and log(*length*)×*area*. Although length-weight curves by INPFC area exhibited some geographic variation (Fig. 5), there was no detectable difference between male and female weight at length. Predicted weight at length was smallest for the Vancouver area and greatest for the Monterey area, whereas length-weight curves from the Columbia and Eureka areas were very similar. Length exponents exceeded 3 for all areas except Vancouver, where few length-weight data were available. As above, the length exponent (with CVs less 2%) was more precisely estimated than the intercept (with CVs of 5–19%). Estimates of parameter bias were less than 1.6% of the parameter estimate in all cases. For each area, the ratio of estimated bias to standard error for the intercept parameter was also low: Vancouver (9%), Columbia (0%), Eureka (0%), and Monterey (5%). Corresponding ratios for the length exponent were also low: 1%, 2%, 7%, and –2%. Thus, parameter bias for the length-weight curves was inconsequential.

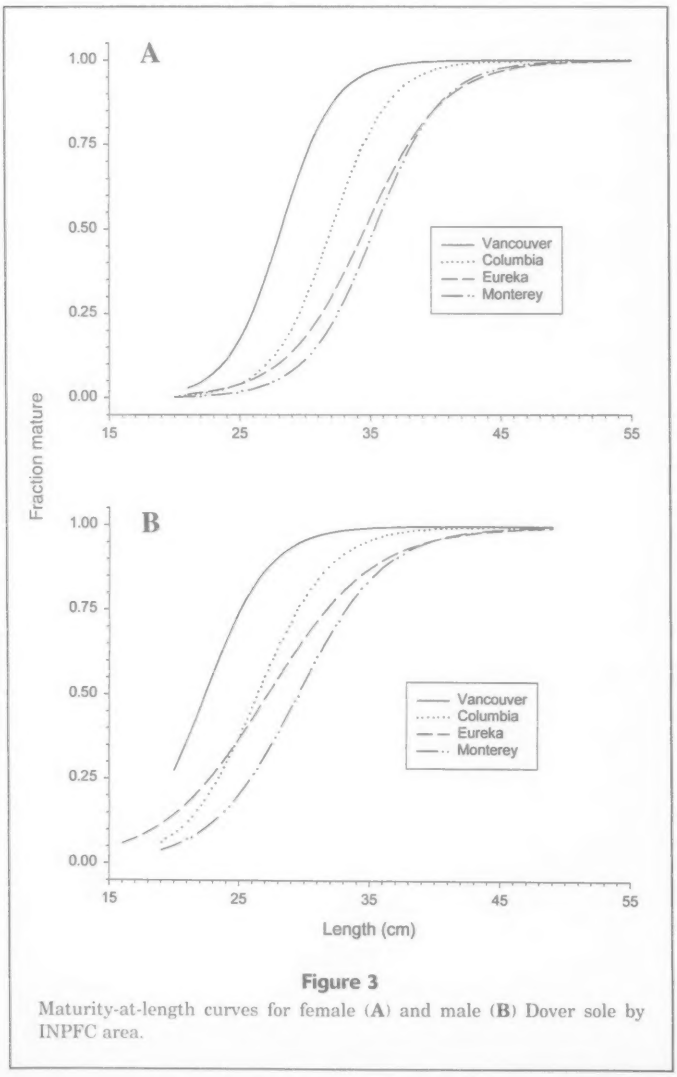

Figure 3

Maturity-at-length curves for female (**A**) and male (**B**) Dover sole by INPFC area.

Discussion

We found that the use of the alternative form of the von Bertalanffy growth curve gave satisfactory parameter estimates that had greater precision than those of the standard form. Bootstrap estimates of standard errors and corresponding coefficients of variation were lower with the alternative form. Ratkowsky (1983) recommended the alternative form used in our study because its parameters were more readily interpreted, it had close-to-linear behavior that facilitated comparisons among data sets, and it was insensitive to the choice of initial parameter values. Our results provide further support for its use.

Variance in size at age of females was 40% greater than that of males. This may result from differences in seasonal patterns of movement between females and males. In particular, Hagerman (1952) noted that commercial Dover sole catches were often segregated by sex and that Dover sole appeared to undertake an inshore feeding migration

Table 4

Maturity-at-length (cm) curves for male and female Dover sole by INPFC area. Standard errors appear immediately below estimates in parentheses. The ratio L_{50}/L_{∞} is reported for comparison with other Pleuronectiformes.

curves by INPFC area	Maturity-at-length L_{50}	β_0	β_1	L_{50}/L_{∞}	n
Male maturity-at-length curves					
All areas[1]	27.1	−6.256	0.2305	0.56	934
	(0.5)	(0.533)	(0.0173)		
Vancouver	22.4	−9.122	0.4078	0.47	77
	(2.1)	(3.854)	(0.1371)		
Columbia	26.4	−9.627	0.3649	0.55	331
	(0.6)	(0.995)	(0.0333)		
Eureka	27.2	−6.717	0.2473	0.57	317
	(0.9)	(0.915)	(0.0291)		
Monterey	29.5	−8.926	0.3029	0.66	209
	(0.7)	(1.051)	(0.0315)		
Female maturity-at-length curves					
All areas	33.4	−9.969	0.2988	0.64	1232
	(0.3)	(0.598)	(0.0169)		
Vancouver	28.2	−13.811	0.4904	0.52	60
	(1.0)	(3.880)	(0.1376)		
Columbia	32.0	−14.315	0.4475	0.61	464
	(0.4)	(1.224)	(0.0367)		
Eureka	34.6	−11.405	0.3299	0.68	415
	(0.5)	(0.878)	(0.0232)		
Monterey	35.3	−13.614	0.3855	0.71	293
	(0.5)	(1.220)	(0.0350)		

[1] INPFC areas sampled in this study: Vancouver, Columbia, Eureka, and Monterey.

Table 5

Maturity-at-age (yr) curves for male and female Dover sole by INPFC area. Standard errors appear immediately below estimates in parentheses. The ratio A_{50}/A_{max} is reported for comparison with other Pleuronectiformes where A_{max} is maximum observed age in our study.

INPFC area	A_{50}	β_0	β_1	A_{50}/A_{Max}
Male maturity-at-age curves				
All areas[1]	5.1	−1.254	0.2438	0.12
	(0.5)	(0.240)	(0.0271)	
Vancouver	3.3	−1.620	0.4838	0.09
	(2.3)	(1.336)	(0.1820)	
Columbia	5.4	−2.314	0.4273	0.13
	(0.5)	(0.456)	(0.0555)	
Eureka	5.2	−1.323	0.2563	0.15
	(0.7)	(0.397)	(0.0467)	
Monterey	6.7	−2.361	0.3510	0.22
	(0.5)	(0.425)	(0.0470)	
Female maturity-at-age curves				
All areas	8.0	−2.733	0.3423	0.17
	(0.2)	(0.256)	(0.0276)	
Vancouver	5.6	−3.353	0.5985	0.19
	(1.1)	(1.343)	(0.1809)	
Columbia	7.5	−4.046	0.5419	0.16
	(0.3)	(0.515)	(0.0588)	
Eureka	8.2	−3.055	0.3710	0.21
	(0.4)	(0.354)	(0.0362)	
Monterey	8.8	−4.094	0.4657	0.21
	(0.4)	(0.496)	(0.0587)	

[1] INPFC areas sampled in this study: Vancouver, Columbia, Eureka, and Monterey.

during spring and an offshore spawning migration in late autumn. Westrheim et al. (1992) inferred from tag recoveries that two major concentrations of Dover sole were present during summer: an inshore group composed of females and small males and an offshore group primarily composed of large males. Jacobson and Hunter (1993) also found that Dover sole segregated by sex in their analysis of bathymetric patterns in population structure. Overall, if large male Dover sole undertake seasonal movements less frequently than females, their growth rates may be expected to be less heterogeneous than those of females that move from the continental slope to the more productive waters of the continental shelf during spring. Seasonal sampling of Dover sole population structure at depth would improve understanding of the relative movements of male and female Dover sole.

As others have suggested (Hagerman, 1952; Hunter et al., 1990; Turnock et al., 1994), we found that Dover sole exhibit sexual dimorphism in growth. In particular, there was a significant difference between male and female growth curves because females attain larger sizes. Mean length of females increased more rapidly than that of males at roughly 5 years of age. The result that females attain greater lengths than males is consistent with Hunter et al. (1990) who also found that values of L_{∞} were greater for females. Although our results were not directly comparable to those of Hunter et al. (1990) because of differences in otolith aging technique and sampling design, asymptotic lengths of females were estimated to be 8% greater than those for male samples in both studies. Some of the growth differences between sexes may result from behavioral differences in feeding and habitat use. Although Dover sole feed more intensively and less selectively on the continental shelf during summer (Pearcy and Hancock, 1978), some older fish may remain in deeper water year round (Hunter et al., 1990). Sexually mature Dover sole are commonly found in the oxygen minimum zone at depths of 600–1000 m (Hunter et al., 1990; Jacobson and Hunter, 1993), where low food and oxygen levels depress metabolism and growth potential (Vetter et al., 1994). Differences between male and female patterns of

growth may result from a differential use of deep-water habitat, where adult males spend more time, on average, in the oxygen minimum zone, or may result from the effects of egg production and spawning on growth and deposition of rings in the annuli of females. In summary, Dover sole exhibit a moderate degree of sexual dimorphism, and differences between sexes become apparent, on average, at about 5 years of age.

In addition to differences between sexes, moderate levels of geographic variation in growth of Dover sole off the west coast were apparent. Growth curves for the Columbia area and for the combined Vancouver, Eureka, and Monterey areas differed for both male and female Dover sole. Asymptotic lengths of males and females from the Columbia area were 3% and 2% greater than those for the combined Vancouver, Eureka, and Monterey areas. Male and female Dover sole from the Columbia area also had lower Brody growth coefficients and larger asymptotic lengths than other areas. These differences, however, were relatively minor and would not be expected to have a substantial impact on target harvest rates if the Dover sole fishery were managed by INPFC areas rather than as a coast-wide unit.

The reason for geographic variation in growth is unknown but probably stems from regional differences in productivity within the California Current. In particular, oceanographic properties of the California Current differ north and south of Cape Blanco (U.S. GLOBEC, 1994), the southern boundary of the Columbia area, and physical differences in the strength and duration of upwelling may affect the growth potential of Dover sole inhabiting these regions. The fact that adult Dover sole are benthic feeders (Pearcy and Hancock, 1978) and are relatively sedentary, having negligible north–south movements (Westrheim et al., 1992), indicates that geographic variation in physical habitat and benthic community structure are probably important determinants of Dover sole growth. Indeed, Jacobson and Hunter (1993) showed that there is relatively more Dover sole habitat off Oregon than off central California.and that depth preferences of Dover sole appear to differ between these regions.

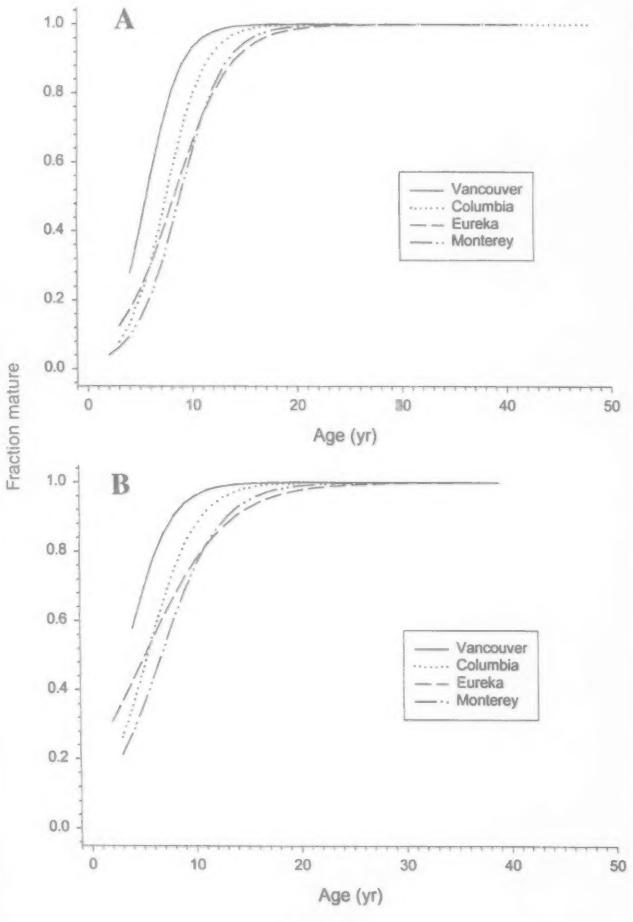

Figure 4

Maturity-at-age curves for female (**A**) and male (**B**) Dover sole by INPFC area.

Alternatively, the cumulative effects of long-term harvest may have also affected the geographic pattern of Dover sole growth because commercial harvests by INPFC area have differed through time. Landings of Dover sole in the Eureka area peaked in the early 1970s, whereas landings in the Columbia, Monterey, and U.S. Vancouver areas peaked in the 1980s (Brodziak, et al. 1997). Although historic size at age of Dover sole has not been documented, some otolith aging data collected off California in the 1940s have provided evidence that mean size at age of males and females may have changed through time (Hagerman, 1952). In particular, Hagerman reported mean sizes at age-5 and age-9 of male Dover sole were 32.3 and 35.5 cm, whereas mean sizes of age-5 and age-9 females were 33.6 and 41.5 cm. In comparison with our estimates, these data suggest that growth may have declined since the 1940s and are consistent with reductions in mean size at age due to fishery-size selection (see Ricker, 1968). Thus, geographic patterns in Dover sole growth may also have been affected by differences in harvest pressure among regions.

Temporal variability of the California Current (Ware, 1995) may have also influenced observed growth, as well as maturation patterns. Research survey samples collected during the 1980s had a higher percentage of

Dover sole that had been spawned prior to a regime shift in the late 1970s (see McGowan et al., 1998) than samples collected during the 1990s. Although temporal changes in growth due to ocean regime may have occurred, such changes would be difficult to detect given the unbalanced temporal and spatial coverage of the available research survey data. Regardless of the mechanism, continued sampling of Dover sole for data on size at age and maturity will be needed to understand whether the observed geographic variation is stable through time.

We found that maturation rates differed between sexes. On average, males matured at a smaller size and at a younger age than did females. This difference might be expected given the sexual dimorphism in Dover sole growth and is consistent with conclusions drawn by Beverton (1992, Fig. 2), who reported that males generally have smaller size at 50% maturity than females within the Pleuronectiformes.

In addition to differences between sexes, we found geographic variation in maturity rates and an apparent latitudinal cline in the median length at maturity of male and female Dover sole. Results were similar for maturity-at-age curves, with the exception of results for Columbia area males. In his review of latitudinal patterns in flatfish reproductive life history, Castillo (1995) found no evidence of a latitudinal trend in age or length at first maturity of Dover sole off Oregon and California. In our study, results suggested that Dover sole mature at smaller size and younger ages at higher latitudes. This finding contrasts with expectations that Dover sole would mature at larger size and older age at higher latitudes (e.g. Castillo, 1995). The apparent trend in Dover sole maturation rates may reflect local adaptation to latitudinal differences in oceanographic properties of the California Current (U.S. GLOBEC, 1994). Nonetheless, sample sizes from some areas (e.g. Vancouver) may have been insufficient to accurately characterize the pattern of maturation in length or age. Also, effects of potential latitudinal differences in the timing of spawning were not accounted for in our study. Thus, although we found some evidence of geographic variation, we recommend further sampling to verify our observed geographic patterns in maturation.

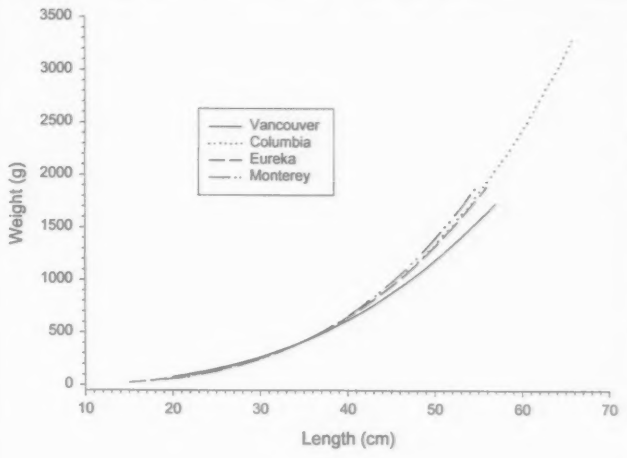

Figure 5

Pooled-sex total length-total weight curves of Dover sole by INPFC area.

Table 6

Estimated parameters and residual variance[1] of Dover sole total length (cm)-total weight (g) curves by INPFC area. Estimated standard errors appear immediately below each estimate in parentheses.

INPFC area	A	B	σ^2	n
All areas	4.0659×10^{-3}	3.2479	1.295×10^{-2}	3019
	(0.1366×10^{-3})	(0.0093)	(0.044×10^{-2})	
Male—all areas	3.7064×10^{-3}	3.2736	1.322×10^{-2}	1470
	(0.1992×10^{-3})	(0.0151)	(0.056×10^{-2})	
Females—all areas	4.4149×10^{-3}	3.2254	1.266×10^{-2}	1549
	(0.2073×10^{-3})	(0.0128)	(0.063×10^{-2})	
Vancouver[1]	13.5571×10^{-3}	2.9093	1.252×10^{-2}	137
	(2.5797×10^{-3})	(0.0521)	(0.040×10^{-2})	
Columbia	3.7610×10^{-3}	3.2676		1645
	(0.1958×10^{-3})	(0.0144)		
Eureka	4.9630×10^{-3}	3.1934		734
	(0.4313×10^{-3})	(0.0235)		
Monterey	2.8550×10^{-3}	3.3484		503
	(0.2146×10^{-3})	(0.0208)		

[1] Residual variance estimates from the generalized linear model are identical for each INPFC area.

Maturity-at-length estimates from our study were consistent with those from other studies of Dover sole maturation. Although maturation criteria and sampling design differed between our study and those of Hunter et al. (1992), estimated median lengths for female maturity were remarkably consistent. In particular, Hunter et al. (1992) estimated female L_{50} to be 33.2 cm, whereas in our study, female L_{50} was estimated to be 33.4 cm. These female L_{50} estimates contrast with earlier estimates that were based on commercial fishery samples in which fish were 36 cm (Hagerman [1952] reported within Hunter et al. [1990]) and 38 cm (Harry [1959]). Although it is unknown whether the earlier estimates are directly comparable to

those of our study because of differences in sampling and maturation criteria, they suggest, however, the possibility that female size at maturity may have declined since the 1950s.

We found no difference between male and female length-weight curves. Male and female length-weight curves were virtually identical for fish less than 50 cm in length. Comparisons between large mature females (>50 cm) and males were not possible because maximum observed size of male Dover sole is about 51 cm. In addition, some geographic variation in length-weight relationships was detected. Estimated length exponents from the allometric equation exceeded 3 for all INPFC areas, with the exception of the Vancouver area, where relatively few samples were collected. Overall, it appeared that Dover sole weight during late autumn, when samples were collected, was not proportional to the cube of fish length. In contrast, Hagerman (1952) found that Dover sole weight was roughly proportional to the cube of length in commercial fishery samples collected throughout the year. Hagerman's estimates may not be comparable to ours owing to differences in sampling and analysis. We recommend year-round collection of Dover sole samples for length-weight analysis to determine whether seasonal and geographic variation are important in predicting mean weight at length in the population.

In comparison with other pleuronectids, we found that Dover sole matured at relatively larger sizes and younger ages. Beverton (1992) reported average ratios of L_{50}/L_{∞} of 0.47 and 0.52 for male and female pleuronectids, whereas comparable values in our study were 0.56 and 0.64. Similarly, male and female ratios of A_{50}/A_{max} of 0.28 and 0.39 from Beverton (1992) were higher than corresponding values of 0.12 and 0.17 in our study. Observed differences with other pleuronectids likely result from the complex life history pattern of Dover sole in the California Current. Dover sole are a relatively late-maturing flatfish. The age at first reproduction (α) that maximizes expected lifetime fecundity for this species is roughly α=15 years, where α=log(1+(3K/M))/K (see Roff, 1991) using K=0.091 for females from our study and a natural mortality rate of M=0.09/yr (Brodziak et al., 1997). In contrast, observed ages at first reproduction for Dover sole range from 4 to 6 years (Castillo, 1995), or roughly 1/3 of the optimal age that would maximize fitness. However, these equilibrium calculations do not account for environmental forcing, and differences between the optimal and observed values probably reflect the importance of environmental variation (Roff, 1982) on the reproductive success of Dover sole. It may be necessary for Dover sole to reproduce as soon as possible to hedge their bets against natural cycling in the survival of pelagic larvae in the California Current (Parrish et al., 1981). In comparison to the pleuronectids reviewed in Beverton (1992), the lower A_{50}/A_{max} ratio of Dover sole may reflect the lack of growth experienced by adults that inhabit the oxygen minimum zone. Similarly, Dover sole may have a higher L_{50}/L_{∞} ratio than other pleuronectids because they achieve most of their potential growth as juveniles while resident on the continental shelf. Overall, maturation rates of Dover sole appear to differ from other pleuronectids and we believe that these differences reflect adaptation of Dover sole to the inherent variability of the California Current.

Acknowledgments

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Genetic structure of two commercial penaeids (*Penaeus californiensis* and *P. stylirostris*) from the Gulf of California, as revealed by allozyme variation

Jorge de la Rosa-Vélez

Facultad de Ciencias Marinas
Universidad Autónoma de Baja California
Km. 106 carretera Tijuana-Ensenada
Ensenada, Baja California 22800, Mexico
E-mail address: jdrosa@bahia.ens.uabc.mx

Roberto Escobar-Fernández

Francisco Correa

Instituto de Investigaciones Oceanológicas
Universidad Autónoma de Baja California
Km. 106 carretera Tijuana-Ensenada,
Ensenada, Baja California 22800, Mexico

Mercedes Maqueda-Cornejo

Javier de la Torre-Cueto

Facultad de Ciencias Marinas
Universidad Autónoma de Baja California
Km. 106 carretera Tijuana-Ensenada
Ensenada, Baja California 22800, Mexico

Abstract—Two commercial shrimp species (*Penaeus californiensis and P. stylirostris*) were sampled along the Gulf of California and crude extracts were assayed electrophoretically to assess allozyme variation and population genetic structure. *Penaeus californiensis*, a more oceanic species, displayed a 12.5% polymorphism (P_{95}) and a 0.023–0.037 expected heterozygosity (H_e) in three sampled populations, whereas *P. stylirostris*, a more coastal species, showed a north–south clinelike pattern in its genetic variability parameters: P_{95} from 15.63% to 31.25% and H_e from 0.038 to 0.086. Differences between species in levels of genetic variation and genotype distribution may be related to differences in habitat during important life cycles stages which reflect the remarkable changes of environmental conditions of coastal lagoons in the Gulf of California. *Penaeus stylirostris* subpopulations appeared more structured (F_{st}=0.372) than those of *P. californiensis* (F_{st}=0.182). A number of private alleles and alternation of the most common allele in several loci account for the outstanding high results of both species. Nei's genetic similarities were computed within species (*P. californiensis* subpopulations, I=0.988–0.997; *P. stylirostris* subpopulations, I=0.929–0.954) and between species (*P. californiensis* × *P. stylirostris*, I=0.674). A dendrogram generated from Nei's genetic similarities segregated the upper Gulf populations of both species from the other two populations (middle Gulf and mouth of the Gulf). This segregation may be the result of the "Island Barrier" hypothesized as segregating other decapods inhabiting the Gulf of California.

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Penaeid shrimp fisheries and hatcheries have undergone an accelerated development during the past three decades (Rosenberry, 1996). Yields of such productive activities are highly appreciated worldwide and have resulted in the economic development of prawn farming in several eastern (e.g. Thailand, Indonesia, Vietnam, China, India, etc.) and Latin American (e.g. Ecuador, Mexico, Colombia, Peru, Panama, etc.) countries.

Business based on penaeid shrimp trading may be considered as having two components: 1) heavy producers, countries, such as those mentioned above, which are mainly exporters, and 2) heavy importers, countries such as those of Europe and the United States of America, where the consumption of imported shrimp has long exceeded landings from their domestic fisheries (Lightner et al., 1997). Moreover, in the way of production (fishing on wild populations vs. rearing in hatcheries), three kinds of producer countries can be recognized: 1) countries that base their shrimp production mainly on their fishery yields (for example, the United States, where farmed shrimps make up only 1% of its production); 2) countries that have focused their shrimp production efforts almost exclusively on hatcheries (for example, Ecuador, where farmed shrimps make up 95% of its shrimp production); and 3) countries that produce shrimps in similar percentages from both wild stocks and hatcheries (for example, Mexico, China, India, and Indonesia) (Lightner et al., 1997).

Shrimp-producing countries, no matter their main way of production, need increasingly to take into account the resource's genetic structure and the variability of fisheries or hatcheries management (Allendorf et al., 1987). Two key questions must be outlined

when a resource is desired to be characterized genetically: 1) What amount of genetic variation is present across its populations? 2) Is the variation homogeneously distributed? This line of research has impelled a number of studies on populations of shrimp species to ensure adequate exploitation and optimal rearing (for a review see Rodríguez-Romero and Rosa-Vélez, 1993).

Our study aimed to characterize the genetic variability and structure of two wild populations of shrimp species, to recognize the actual genetic pool currently segregating in them, and to render information to design rearing strategies based on existing genetic variability.

Penaeus (Farfantepenaeus) californiensis Holmes is an oceanic species distributed in the eastern Pacific, San Francisco Bay, U.S.A., to Sachura Bay, Peru and Galapagos Islands, Ecuador (Rodriguez de la Cruz, 1976). Adults are found up to 220 m deep, although the peak of abundance occurs at 55 m on silt-clay or sand-silt bottoms (Rodríguez de la Cruz and Rosales, 1970). *Penaeus (Litopenaeus) stylirostris* Stimpson is a more coastal species distributed from the upper Gulf of California, Mexico, to Tumbes, Peru. Adults are found in shallow waters around the mouth of coastal lagoons, up to 40 m deep (CICTUS, 1985), where they are more abundant.

Life cycles are similar for both species but there is one very distinctive difference: *P. californiensis* can complete its whole life cycle in the marine environment, whereas *P. stylirostris* must spend part of its life cycle (postlarval and juvenile stages) as an inhabitant of coastal lagoons. In brief, for both species, females deposit eggs in demersal zones where they undergo total segmentation in 12–15 hours. The outcome is a planktonic larva that metamorphoses through five naupliar, three protozoean, and three mysis stages, before reaching the semibenthic postlarval stage. Once the rostral form is accomplished, the animal is considered a juvenile and is totally benthic. The complete cycle may take12–17 days (Rodríguez de la Cruz and Rosales, 1970).

In our study we ascertained different levels of genetic variation between species, a clinelike pattern of genetic variability in the more coastal species, and significant genetic structure among subpopulations of both species.

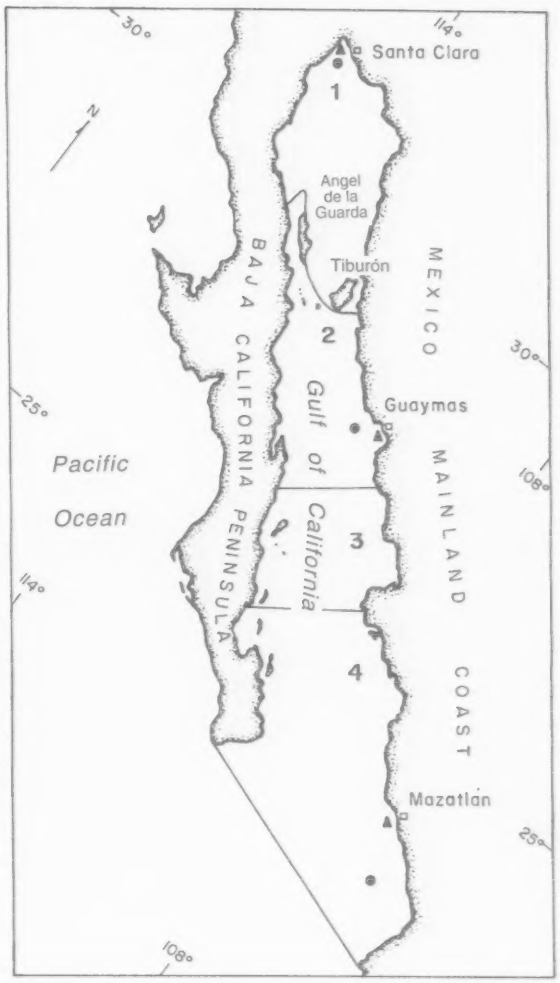

Figure 1

Map of the Gulf of California showing its subdivision (after Round, 1967): 1 = upper Gulf; 2 = middle Gulf; 3 = lower Gulf; and 4 = mouth of the Gulf; and the sampling locations: ▲ = *Penaeus stylirostris*, and ● = *Penaeus californiensis*.

Materials and methods

Samples of *Penaeus californiensis* were obtained in November 1995 by means of bottom trawling nets operated from commercial shrimp fishing vessels performing standard catching efforts (average trawling time: 1 hour; trawling speed: 2 knots), in the following locations: south of Santa Clara Port (31°34′N, 114°19′W); west of Guaymas Port (27°50′N, 111°05′W); and southwest of Mazatlan Port (22°27′N, 106°44′W). Samples of *P. stylirostris* were caught in September 1995 with a cast net thrown from small boats in the following shallow coastal areas: off Santa Clara Port (31°44′N, 114°19′W); off Guaymas Port (27°54′N, 110°55′W); and off Mazatlan Port, (23°12′N, 106°30′W). The samples covered three out of four distinctive areas (called here "upper Gulf, middle Gulf, lower Gulf, and mouth of the Gulf") according to Round (1967; Fig. 1). Samples were frozen (–20°C) and shipped to the laboratory, where they were stored at –75°C until dissection.

Soft tissues from head and abdominal muscle from adult specimens were separated and homogenized in 1 to 2 volumes of cold buffer prepared with 0.1 M Tris-HCl, pH 7.00 + NAD^+ + $NADP^+$ + PVP (10:1:1:100; v:p:p:p). Homogenates were spun (12,000 × g) at 4°C, for 20 min. Supernatants were stored at –75°C until needed.

Electrophoretic assays were performed on 12.5% starch gels (Sigma Chemical Co., St. Louis, MO) in a horizontal apparatus that was placed in the refrigerator (4°C). Three

buffer systems were used to resolve 16 enzymatic systems and muscular protein: continuous tris-citrate buffer, pH 8.0 (TC8) following Selander et al. (1971), 150 V, 6 h; discontinuous tris-citrate, pH 8.3-sodium borate buffer, pH 8.65 (POU) according to Poulik (1957), 250 V, 5 h; and continuous tris-EDTA-borate, pH 8.0 (TEB) following Shaw and Koen (1968), 200 V, 6 h. Tissue sources, electrophoresis systems employed to resolve each enzyme or muscular protein, and number of loci resolved in each enzyme system are listed in Table 1. Staining procedures were accomplished according to the methods of Schaal and Anderson (1974), Shaw and Prasad (1970), Shaw and Koen (1968), Abreu-Grobois (1983), and Rosa-Vélez (1986).

Allelomorphs were named A to F depending on their anodal mobility, A being the fastest one. Zymogram interpretation was achieved following recommendations by Utter et. al (1987). In those cases where more than one zone of activity was present in the gel, genetic hypotheses were constructed to ensure correct interpretation. The more complex pattern was displayed by the group of esterases, which was interpreted by standardizing procedures. These involved gel staining with each of the esters used in the staining mixture (a-naphtyl acetate [black bands] and b-napthyl acetate [red bands]), but in separate assays, followed by a joined assay of the same sample, as Laubier et al. (1984) suggested.

Swofford's (1989) BIOSYS-1 software was fed with raw genotypic data from electropherograms to obtain allelic frequencies, proportion of polymorphic loci at the 95% level, observed and unbiased expected (Nei, 1978) heterozygosity, chi-square goodness-of-fit test for testing conformity to the Hardy-Weinberg equilibrium (H-W equilibrium) of variable loci, and Nei's (1978) unbiased genetic similarity and distance.

The same set of raw data was used with GENEPOP (versus 1.2) (Raymond and Rousset, 1995), to compute an unbiased estimate of the P-value of an F_{st}-based exact test for the distribution of genotypes by means of the Markovian chain method. PHYLIP's software (versus 3.5) was used to perform bootstrap resampling of gene frequencies to obtain a genetic distance UPGMA (unweighted pair-group method with arithmetic averaging) dendrogram. A Bonferroni correction was applied where multiple tests were carried out.

Results

A total of 32 loci were resolved from 16 enzyme systems and muscular protein. Twenty loci (*Acph-1, Aph-2, Gdh, Got-1, Got-2, G3pd, Gpd, Idh, Ldh, Mdh-1, Mdh-2, Me, Pt-1, Pt-2, Pt-4, Pt-5, Pt-6, Sdh-1, Sdh-2,* and *Xdh*) were monomorphic across all populations sampled. Protein polymor-

Table 1

Electrophoretic conditions, tissues assayed and number of loci resolved in the allozymic variation study of *Penaeus californiensis* and *P. stylirostris*. E.C. = Enzyme Commission.

Enzyme	E.C. no.	Tissue[1]	Buffer system[2]	Staining recipe[3]	Genetic locus	No. of loci scored
Acid phosphatase	3.1.3.2	C	B	SP	*Acph*	2
Alkaline phosphatase	3.1.3.1	C,M	A	SK	*Aph*	3
Esterase	3.1.1.1	C	C	SP	*Est*	5
Glucose-6-phosphate dehydrogenase	1.1.1.49	M	C	SA	*G6pd*	1
Glutamate dehydrogenase	1.4.1.3	M	C	SA	*Gdh*	1
Glutamic oxalacetic transaminase	2.6.1.1	M	A	SA	*Got*	2
Glyceraldehyde-3-phosphate dehydrogenase	1.2.1.12	M	C	SA	*G3pd*	1
α-Glycerophosphate dehydrogenase	1.1.1.8	M	C	SA	*Gpd*	1
Isocitrate dehydrogenase	1.1.1.42	M	C	AG	*Idh*	1
Lactate dehydrogenase	1.1.1.27	M	C	SP	*Ldh*	1
Leucinamino peptidase	3.4.11.1	C	A	SP	*Lap*	1
Malate dehydrogenase	1.1.1.37	M	C	SA	*Mdh*	2
Malic enzyme	1.1.1.40	M	A	SA	*Me*	1
Phosphoglucomutase	5.4.2.2	M	A	SA	*Pgm*	1
Total protein	—	C,M	B	RV	*Pt*	6
Sorbitol dehydrogenase	1.1.1.14	M	A	SA	*Sdh*	2
Xantine dehydrogenase	1.2.1.37	M	A	SA	*Xdh*	1

[1] C = cephalothorax; M = muscle.

[2] A = tris-citrate, pH 8.0 (Selander et al., 1971); B = tris-citrate, pH 8.3-sodium borate, pH 8.65 (Poulik 1957; C = Tris-EDTA-borate; pH 8.0 (Shaw and Koen, 1968).

[3] SA = Schaal and Anderson (1974); SP = Shaw and Prasad (1970); SK = Shaw and Koen (1968); AG = Abreu-Grobois (1983); RV = Rosa-Vélez (1986).

phism ($P \leq 0.95$) was 0.125 for *P. californiensis* in the three populations sampled along the Gulf of California, unlike *P. stylirostris* that showed a clinelike pattern with increasing polymorphism from 0.156 in the upper Gulf population to 0.312 in the mouth of the Gulf. The genetic diversity, reported as expected heterozygosity, was quite homogeneous along the surveyed distribution of *P. californiensis* and showed a gradual northern–southern increase in *P. stylirostris*. (Table 2).

After the Bonferroni correction for multiple tests was applied ($\alpha' = 0.00142$), only *Est-2* was out of H-W equilibrium in at least one population of each species, and *Pgm* and *Pt-3* displayed the same pattern in *P. stylirostris*, all of them accounting for heterozygote deficiency (Table 2).

Four loci (*Aph-3, Est-1, Est-4,* and *Est-5*) in the upper population of *P. stylirostris* showed $D = -1.000$ values (see Table 2); however, four loci had to be considered monomorphic because the polymorphism criterion applied was the most conservative (P_{95}; a locus is considered polymorphic only when the frequency of the most common allele is ≤0.95). In most of these cases only one or two individuals were scored as homozygotes for the alternative allele. Such a low frequency may not be significant for the evolutionary process owing to the high probability of disappearance through random processes in just a few generations.

On the other hand, in spite of the high frequencies of both alleles ($p = 0.5$), only one heterozygous individual was scored for the diallelic locus *Aph-1* in the upper population of *P. stylirostris*, resulting in a highly significant heterozygote deficiency.

Standardized variance (F_{st}) analysis was achieved among subpopulations within species (Table 3). *Penaeus californiensis* showed a lesser degree of genotypic differentiation among its populations ($F_{st} = 0.182$) than *P. stylirostris* ($F_{st} = 0.372$). This result is possibly related to the mean frequency of private alleles (*sensu* Barton and Slatkin, 1986) in their populations ($p = 0.096$ in *P. californiensis*; and $p = 0.214$ in *P. stylirostris*), even though both figures were notably high. Three loci accounted for differences in the subpopulations of *P. californiensis*: *Aph-3, Est-1,* and *Est-2*. The higher genetic variability displayed by *P. stylirostris* produced a more complex pattern of genotypic differentiation where ten loci accounted for significant differences among subpopulations (*Acph-3, Est-1, Est-2, Est-3, Est-4, Est-5, G6pd, Lap, Pgm, and Pt-3*).

Genetic similarities among subpopulations showed a similar pattern in both species (Table 4); there was a closer resemblance between the middle Gulf and the mouth of the Gulf populations of both species than with the upper Gulf population. This pattern can be visualized in the dendrogram (Fig. 2), where the upper Gulf population of both species segregates from the other two, which are clustered together.

Furthermore, a different level of similarity among subpopulations within species is clearly noticeable (Table 4). *Penaeus californiensis* showed a higher level of similarity among its subpopulations (*I* range: 0.988–0.997) than *P. stylirostris* (*I* range: 0.929–0.954). Genetic similarities between species rendered a clustering level of 0.674 (Fig. 2, Table 4).

Discussion

Two results are of particular interest: a north–south clinelike gradual increase in genetic variability in the more coastal species and the finding of a heterogeneous distribution of genotype frequencies in both assayed species. Most of the previous studies on *Penaeus* species around the world have depicted a general pattern of low homogeneous genetic variability. For example, Mulley and Latter (1980) reported heterozygosity values ranging between 0.006 and 0.033 in Australian penaeids (four species of *Metapenaeus* and six of *Penaeus*). These data were confirmed by subsequent studies: Richardson (1982) found an average heterozygosity of 0.028 in six populations of *P. latisculatus*, and Tam and Chu (1993) reported an observed heterozygosity range of 0.007–0.049 in some species of *Penaeus* and *Metapenaeus* from the South China Sea. *Penaeus japonicus* exhibited one of the highest heterozygosity values ($H_0 = 0.047 \pm 0.029$) among the species surveyed in that study. However there are other reports of even greater heterozygosity in populations of that species transported to European hatcheries as broodstock ($H_0 = 0.102$, Sbordoni et al., 1986; $H_0 = 0.071$, Laubier et al., 1984).

For penaeid species occurring in the western hemisphere, Lester (1979) reported heterozygosities between 0.070 and 0.089 for three commercial penaeids of the Gulf of Mexico. Very similar data for the same species were later reported by Labacena et al. (1994). Lester (1983) also studied one population of each species, *P. vannamei* (from Chomes, Costa Rica) and *P. stylirostris* (from Guaymas, México), which dwell along the northeastern Pacific coast, and reported heterozygosity values of 0.02 and 0.06, respectively. Sunden and Davis (1991) reported heterozygosity values for *P. vannamei* samples from Mexico, Panama, Ecuador, and one farmed population at a Texas hatchery, which were 0.0173, 0.0172, 0.0208, and 0.0111, respectively.

Levels of genetic variability of the species that we studied were not out of the range of those of previous estimations. It must be noticed, in addition, that *P. californiensis* showed a lower, narrower heterozygosity range (0.023 ±0.014–0.037 ±0.012) than *P. stylirostris* (0.038 ±0.021–0.086 ±0.027). The latter might be explained by the different habitats that each species occupies during its life cycle. This important difference may also be related to the clinelike pattern of the heterozygosity values in *P. stylirostris*, whereas the genetic variability of *P. californiensis* could be evidence of the more stable oceanic conditions that this species experiences during its life span. *Penaeus stylirostris* appears to reflect the environmental variability of the coastal lagoons, which it penetrates during a critical stage of its life cycle. Latitudinal variability of hydrological, ecological, and productivity conditions characterize coastal lagoons along the eastern coast of the Gulf of California. The upper zone's coastal lagoons (Fig. 1) are located in an arid region where vegetation is scarce; around the lagoons, some halophytes and sea grasses predominate. Productivity in these basins depends almost exclusively on microalgae (phytoplankton and microphytobenthos) (Contreras, 1985). To the south, through the

Table 2

Genetic variation of six naturally occurring populations of *Penaeus californiensis* (3) and *P. stylirostris* (3) throughout the Gulf of California (upper, middle and mouth of Gulf). Population names correspond to designated zones of the Gulf (see Fig. 1); n = the number of genes assayed, H = the frequency of observed heterozygotes, D = Selander's coefficient of deviation. Significances of goodness-of-fit chi-square tests (after Bonferroni correction) are given as usual (*=$P \leq 0.05$; ***=$P \leq 0.001$).

			Penaeus californiensis			*Penaeus stylirostris*		
Locus		Allele	Upper	Middle	Mouth	Upper	Middle	Mouth
Acph-3	*n*		76	44	92	96	42	28
		A	1.000	1.000	1.000	1.000	1.000	0.429
		B	0.000	0.000	0.000	0.000	0.000	0.321
		C	0.000	0.000	0.000	0.000	0.000	0.250
	H		0.000	0.000	0.000	0.000	0.000	0.429
	D		0.000	0.000	0.000	0.000	0.000	–0.365
Aph-1	*n*		90	48	96	96	48	32
		A	1.000	1.000	1.000	0.510	0.250	0.406
		B	0.000	0.000	0.000	0.490	0.750	0.594
	H		0.000	0.000	0.000	0.021	0.417	0.438
	D		0.000	0.000	0.000	–0.959***	0.088	–0.121
Aph-3	*n*		90	34	90	92	48	32
		A	0.067	0.000	0.021	0.978	1.000	1.000
		B	0.889	0.765	0.947	0.022	0.000	0.000
		C	0.044	0.000	0.032	0.000	0.000	0.000
		D	0.000	0.235	0.000	0.000	0.000	0.000
	H		0.178	0.235	0.022	0.000	0.000	0.000
	D		–0.136	–0.365	–0.662	–1.000***	0.000	0.000
Est-1	*n*		76	38	96	84	36	28
		A	0.737	0.342	0.156	0.976	0.389	0.643
		B	0.171	0.632	0.646	0.024	0.500	0.214
		C	0.092	0.026	0.198	0.000	0.111	0.143
	H		0.237	0.211	0.333	0.000	0.444	0.286
	D		–0.443	–0.576	–0.365	–1.000***	–0.263	–0.471
Est-2	*n*		82	48	96	88	44	32
		A	0.024	0.000	0.000	0.000	0.000	0.000
		B	0.012	0.104	0.083	0.000	0.000	0.000
		C	0.061	0.229	0.052	0.398	0.023	0.344
		D	0.573	0.667	0.854	0.602	0.909	0.625
		E	0.329	0.000	0.010	0.000	0.068	0.031
	H		0.244	0.625	0.292	0.159	0.182	0.125
	D		–0.569*	0.243	0.107	–0.672*	0.055	–0.753
Est-3	*n*		72	38	96	74	44	32
		A	0.083	0.053	0.052	0.203	1.000	1.000
		B	0.889	0.947	0.948	0.797	0.000	0.000
		C	0.028	0.000	0.000	0.000	0.000	0.000
	H		0.111	0.105	0.104	0.351	0.000	0.000
	D		0.458	0.028	0.044	0.072	0.000	0.000
Est-4	*n*		76	42	94	86	34	24
		A	1.000	1.000	1.000	0.953	0.853	0.292
		B	0.000	0.000	0.000	0.047	0.147	0.708
	H		0.000	0.000	0.000	0.000	0.176	0.250
	D		0.000	0.000	0.000	–1.000***	–0.317	–0.420

continued

mouth of the Gulf, subtropical conditions prevail; abundant fringing vegetation, dominated by four species of mangroves, contributes a huge amount of organic matter that triggers a complementary source of organic production within the detritus chain. Biodiversity indices rise and trophic resources become diversified (González-Farias and Mee, 1988; Flores-Verdugo, 1990). Hence, it is plausible to assume that complexity of ecological webs increases from the northern to the southern coastal zone of the Gulf of California. A parallel gradual increment in heterozygosity in the populations of *P. stylirostris* may be related to that ecological feature. However, Burton (1983) has stated that a direct relation between high heterozygosity and high ecological complexity is very difficult to demonstrate,

Table 2 (continued)

			Penaeus californiensis			*Penaeus stylirostris*		
Locus		Allele	Upper	Middle	Mouth	Upper	Middle	Mouth
Est-5	*n*		96	46	96	94	46	30
		A	1.000	1.000	1.000	0.957	0.022	0.767
		B	0.000	0.000	0.000	0.043	0.717	0.200
		C	0.000	0.000	0.000	0.000	0.261	0.033
	H		0.000	0.000	0.000	0.000	0.130	0.133
	D		0.000	0.000	0.000	–1.000***	–0.694	–0.653
G6pd	*n*		96	48	96	90	38	30
		A	1.000	1.000	1.000	1.000	1.000	0.767
		B	0.000	0.000	0.000	0.000	0.000	0.100
		C	0.000	0.000	0.000	0.000	0.000	0.133
	H		0.000	0.000	0.000	0.000	0.000	0.267
	D		0.000	0.000	0.000	0.000	0.000	–0.329
Lap	*n*		96	48	96	92	48	32
		A	1.000	1.000	1.000	0.272	0.458	0.688
		B	0.000	0.000	0.000	0.728	0.542	0.313
	H		0.000	0.000	0.000	0.543	0.500	0.500
	D		0.000	0.000	0.000	0.358	–0.014	0.127
Pgm	*n*		96	48	94	88	48	32
		A	1.000	1.000	1.000	0.125	0.104	0.094
		B	0.000	0.000	0.000	0.795	0.292	0.281
		C	0.000	0.000	0.000	0.000	0.188	0.531
		D	0.000	0.000	0.000	0.000	0.333	0.094
		E	0.000	0.000	0.000	0.034	0.083	0.000
		F	0.000	0.000	0.000	0.045	0.000	0.000
	H		0.000	0.000	0.000	0.136	0.208	0.315
	D		0.000	0.000	0.000	–0.613*	–0.728*	–0.513
Pt-3	*n*		96	48	96	96	48	32
		A	1.000	1.000	1.000	0.000	0.250	0.063
		B	0.000	0.000	0.000	1.000	0.750	0.938
	H		0.000	0.000	0.000	0.000	0.083	0.000
	D		0.000	0.000	0.000	0.000	–0.782*	–1.000
Number of loci studied			32	32	32	32	32	32
Mean number of individuals per locus			45.8 ±0.6	22.3 ±0.7	46.2 ±1.5	44.7 ±1.1	22.0 ±0.6	15.7 ±0.2
Mean number of alleles per locus			1.31 ±0.16	1.19 ±0.09	1.25 ±0.13	1.38 ±0.12	1.44 ±0.16	1.53 ±0.16
Polymorphism (P_{95})			12.50	12.50	12.50	15.63	25.00	31.25
H_0			0.024 ±0.012	0.037 ±0.021	0.023 ±0.014	0.038 ±0.021	0.067 ±0.025	0.086 ±0.027
H_e			0.044 ±0.023	0.046 ±0.024	0.030 ±0.018	0.075 ±0.027	0.109 ±0.038	0.145 ±0.041

and therefore, correlation should not be taken as conclusive evidence for causation.

Several reports have stated a small probability of encountering genetically "differentiated" stocks in *Penaeus* species, mainly due to their low variability and the apparent homogeneous allele distributions among the subpopulations (Lester, 1979, 1983; Mulley and Latter, 1981a, 1981b; Richardson, 1982). However, Sunden and Davis (1991) could trace a slight geographic differentiation across the range of *P. vannamei*. They detected at least one unique allele in each wild population. Tam and Chu (1993) attributed the higher genetic similarity shown between the species pair *P. merguiensis* and *Metapenaeus ensis* to the genetic differentiation among populations of the same species. In addition, some allozyme variation was observed among populations of *Metapenaeus benettae* (Salini, 1987) in Australia and *P. kerathurus* in the Mediterraenean (Mattocia et al., 1987). From later studies, it was noticed that when the allozymes surveys were performed over larger geographical scales, substantially higher significant variation and differentiation among populations was found. Such is the case for the wild populations of *P. monodon* along the Australian coast (Benzie et al., 1992), where expected heterozygosities have ranged between 0.053 and 0.103, and significant genetic differences have existed among Australian populations.

The use of more variable markers such as mtDNA genes have confirmed the allozymic findings on the structuring of *P. monodon* populations in Australia (Benzie et al., 1993), and *P. notialis* and *P. schmitti* in the South American Atlantic coast (Machado et al., 1993).

From our data, subpopulations of both species appear genetically differentiated in terms of significant values of standardized variance of their genotypic distributions (Table 3). Two reasons seem to account for such a result: 1) private alleles exist in about every polymorphic locus (75% in both species), and 2) the most frequent allele alternates among subpopulations of the same species in several loci (see Table 2).

Heterogeneity among subpopulations is commonly explained as a lack of genetic flow (see Slatkin, 1985, for a review). Nonetheless, penaeids can be considered vagile species because they have two dispersal phases, the planktonic larvae and the vagile adult. Lester (1979) imputes this characteristic to the high levels of genetic similarity among the penaeids populations of the Gulf of Mexico.

Although penaeids are capable of being displaced, geographical barriers must prevent their movement. The Gulf of California is now considered as a much more complex ecosystem than it was formerly believed: Santamaría-Del Angel et al. (1995) proposed 14 biogeographic subdivisions in the Gulf on the basis of satellite images describing concentrations of photosynthetic pigments. Likewise, González-Farias et al. (1995) described complicated patterns of carbon turn-over throughout the Gulf from the analysis of organic matter and heterotrophic bacteria. The upper Gulf region is a very unique environment where the Colorado River drained until about fifty years

Table 3

Wright's standardized variance (F_{st}) of populations within species. Statistical significance in brackets (ns=not significant; **=$P \leq 0.01$; ***=$P \leq 0.001$).

Loci	*P. californiensis*	*P. stylirostris*
Acph-3	—	0.510(***)
Aph-1	—	0.054(ns)
Aph-3	0.094(***)	–0.022(ns)
Est-1	0.278(***)	0.384(***)
Est-2	0.134(***)	0.128(**)
Est-3	–0.005(ns)	0.756(***)
Est-4	—	0.514(***)
Est-5	—	0.650(***)
Gdh-1	—	–0.009(ns)
G6pd	—	0.207(***)
Lap	—	0.149(***)
Pgm	—	0.264(***)
Pt-3	—	0.210(**)
Mean values	0.182(***)	0.372(***)

Table 4

Nei's genetic similarity (above diagonal *****) and distance (below diagonal *****) among six populations of two penaeid species, *Penaeus californiensis* and *P. stylirostris*, throughout the Gulf of California (upper, middle, and mouth of Gulf).

		Penaeus californiensis			*Penaeus stylirostris*		
	Population source	Upper	Middle	Mouth	Upper	Middle	Mouth
Penaeus californiensis	Upper	*****	0.991	0.988	0.690	0.654	0.691
	Middle	0.009	*****	0.997	0.632	0.656	0.686
	Mouth	0.012	0.003	*****	0.672	0.655	0.679
Penaeus stylirostris	Upper	0.371	0.383	0.397	*****	0.929	0.936
	Middle	0.425	0.422	0.423	0.074	*****	0.954
	Mouth	0.370	0.377	0.387	0.067	0.047	*****

ago, when the Hoover Dam was constructed up river and flow was severely restricted. Presently, hypersaline conditions prevail in the upper Gulf region. This dynamic and extreme environment is topographically bounded to the south by a submarine range. Tiburón and Angel de la Guarda Islands are the heights of this submarine range (Fig. 1); south of these islands the Gulf increases in depth to around 3000 m in the Guaymas Basin. Thus, the islands may be considered a geographical or ecological boundary that reduces the free flow of penaeids. Correa-Sandoval and Carvacho-Bravo (1992) came to a similar conclusion when they described the distribution pattern of brachyuran crabs in the Gulf of California.

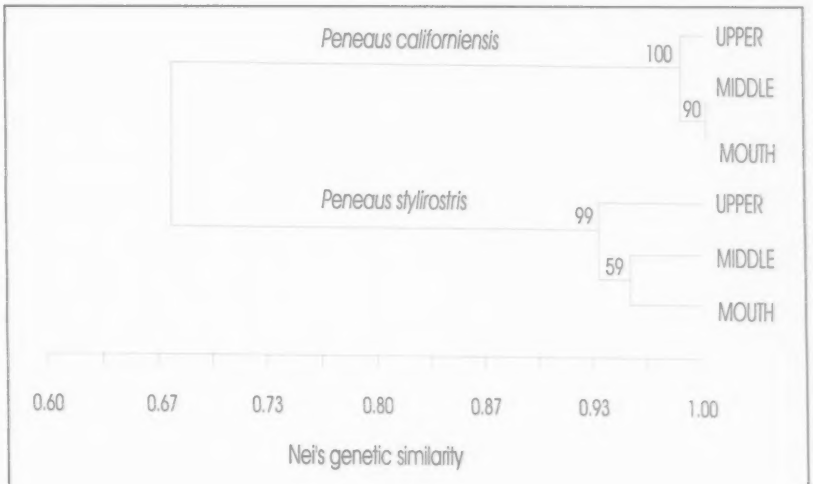

Figure 2

Bootstrapped dendrogram generated from a Nei's (1978) genetic similarities matrix (UPGMA algorithm) between species and their subpopulations. Data based on 32 loci.

In some populations of both species, three loci (*Aph-1*, *Est-2*, and *Pgm*) were found to be out of H-W equilibrium according to the chi-square goodness-of-fit test. Two of the common causes of heterozygote deficiency, as discussed by Zouros and Foltz (1984), can be invoked here: 1) the Wahlund effect, because some genetic structure has been demonstrated in both species, at least in the geographic range that we studied; thus, different genetic compositions taking part in reproductive events, will yield such a pattern; and 2) selection against heterozygotes, a hypothesis that is difficult to prove, but is feasible owing to very recent environmental modification (ca. half a century). Homozygous genotypes may be selected if they perform better under extreme conditions with no drastic gene erosion during the little time elapsed since environmental alterations began. For example, *Aph-1* displays a ca. 50% frequency of the two segregating alleles, which allows us to expect high heterozygote frequency. However, the sample lacked these genotypes almost completely. With no additional evidence to discard either of the above, a third one, i.e. the presence of a null allele segregating in this population, may also be invoked. Further evidence from breeding experiments among individuals of this population is needed to evaluate this supposition.

Additional evidence of the divergence of populations (remarkably, populations of both species dwelling in the upper Gulf) is given by Nei's genetic similarity (Table 4; Fig. 2). It is evident from the dendrogram that 1) there is a clear subdivision in both within-populations dendrograms that distinguishes the populations inhabiting the upper Gulf (hence, it is not only the previously discussed characteristic of heterozygote deficiency that segregates these populations from the rest, but the distribution of their genes too) and 2) a subdivision between species where the degree of genetic similarity is similar to those previously reported in other penaeid species. Average genetic similarities among species within *Penaeus* genera were 0.65 ±0.08, and 0.69 ±0.08 within *Metapenaeus* (Mulley and Latter, 1980). Similar values (I=0.66) were found between two forms of brachyuran freshwater crabs from South Africa (Stewart and Cook, 1998).

The characteristic genetic features we found provide additional support for the recent scheme proposed by Pérez-Farfante and Kensley (1997). Their proposition, regarding the reorganization of American shrimps in the family Penaeidae, involves the promotion of an existing subgenus to genus, i.e. *Penaeus californiensis* would become *Farfantepenaeus californiensis*, and *Penaeus stylirostris* would change to *Litopenaeus stylirostris*. However, more evidence must be compiled to support this reclassification.

Complexity of the Gulf of California ecosystem, as well as the biological features described for each species, may account for the greater degree of genetic structure in the species that inhabit it. Fisheries and hatcheries managers can take advantage of such information, for example, by defining stocks or selecting the more variable populations to be submitted to artificial selection programs in the aquaculture scheme.

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Indices of larval king mackerel (*Scomberomorus cavalla*) abundance in the Gulf of Mexico for use in population assessments

Christopher T. Gledhill

Joanne Lyczkowski-Shultz

Southeast Fisheries Science Center
National Marine Fisheries Service, NOAA
3209 Frederic St.
Pascagoula, Mississippi 39568-1207
E-mail address (for C. T. Gledhill): Christopher.T.Gledhill@noaa.gov

Abstract–The stock status of the Gulf of Mexico migratory group of king mackerel (*Scomberomorus cavalla*) is currently evaluated by using age-based sequential virtual population analysis (VPA). We examined king mackerel larval occurrence and abundance indices from annual ichthyoplankton surveys, developed an age-adjusted abundance index, and questioned whether larval indices of abundance are useful for calibrating the king mackerel VPA. Gulf of Mexico king mackerel larval occurrence and abundance increased over a fourteen-year time series from 1982 to 1995 and were highly correlated with spawning stock size. Correlations between stock size and larval occurrence, and between stock size and larval abundance, were 0.82 and 0.84, respectively. The correlation between larval occurrence and stock size for the years 1986–95 increased to 0.91, owing to the addition in 1986 of a fall survey with added coverage during peak spawning. Daily instantaneous mortality rate (Z) was estimated by regression of larval catch curves. Although a large amount of interannual variability in mortality rates was noted, no statistical differences were detected among years. The instantaneous daily mortality rate estimated by pooling all years, $Z = 0.53$, was used to develop an age-adjusted index for king mackerel in order to eliminate the influence of variable larval age composition among years. This adjusted index did not improve correlations between stock size and larval abundance (r=0.78). For now, indices of larval occurrence and unadjusted larval abundance from ichthyoplankton collections reflect trends in spawning stock size and provide useful variables for calibrating the king mackerel VPA.

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The king mackerel (*Scomberomorus cavalla*), a western Atlantic member of the family Scombridae, ranges from Massachusetts to Brazil (Shipp, 1986). This highly migratory, coastal pelagic species can attain a maximum size of 1.7 m and 45 kg (Robins and Ray, 1986) and ages of more than 20 years (DeVries and Grimes, 1997). King mackerel support valuable commercial and recreational fisheries that are regulated in the southeastern coastal states and Gulf of Mexico under the Coastal Migratory Pelagic Resources Fishery Management Plan. These fisheries were largely unregulated in the late 1970s and early 1980s when fishing mortality was high, and thus stock size was reduced. As a result, management by quota was implemented in the 1985–86 fishing year. The current management regime for king mackerel fisheries recognizes only two stocks off the U.S. southeast coast: an Atlantic migratory group and a Gulf of Mexico migratory group. There is, however, some disagreement as to whether there are one or two distinct stocks in the Gulf of Mexico (Johnson et al., 1994; DeVries and Grimes, 1997; Gold et al., 1997; Roelke and Cifuentes, 1997).

Reproduction in this highly fecund, serial spawning species occurs from May through early October and peaks in September along both the U.S. Gulf of Mexico and southeast Atlantic coasts (McEachran et al., 1980; Finucane et al., 1986; Grimes et al., 1990). Data on the abundance and distribution of king mackerel larvae indicate that spawning occurs chiefly over the mid to outer continental shelf of the northern Gulf of Mexico (McEachran et al., 1980; Grimes et al., 1990). Grimes et al. (1990) suggested that spawning occurs over shallower depths in the region from west Louisiana to northwest Florida and may be associated with oceanographic features, especially the discharge plume of the Mississippi River. Absolute growth rates of king mackerel larvae were observed to range from 0.54 to 1.33 mm per day and were slightly higher for larvae from the Mississippi River plume when compared to other locations in the Gulf and southeast Atlantic coast (DeVries et al., 1990).

Population size of Gulf-group king mackerel is estimated biennially by scientists of the Mackerel Stock Assessment Panel (Gulf of Mexico and South Atlantic Fishery Management Councils) using an age-based sequential virtual population analysis (VPA). This VPA is implemented by using ADAPT (Conser and Powers, 1990; Powers and Restrepo, 1993). The king mackerel VPA is calibrated or tuned by using various indices of abundance based on fisheries dependent catch-per-unit-of-effort and fisheries independent resource survey data. Survey estimates of annual abundance and frequency of occurrence of king mackerel larvae were first considered as tuning variables for the king mackerel VPA by the 1996 Mackerel Stock Assessment Panel.[1] Although fre-

[1] Mackerel Stock Assessment Panel. 1996. 1996 Report of the Mackerel Stock Assessment Panel. Gulf of Mexico Fishery Management Council, Lincoln Center, Suite 331, 5401 West Kennedy Blvd, Tampa, FL 33609 and South Atlantic Fishery Management Council, Southpark Bldg., Suite 306, 1 Southpark Circle, Charleston, SC 29407.

quency of occurrence was ultimately accepted as a tuning variable, abundance was not because larval catches had not been adjusted for age. Interannual differences in age composition of sampled larvae could contribute a large amount of variation in estimates of mean annual abundance because of the exponential decline in numbers of larvae with age. Furthermore, it was thought that survey estimates of larval abundance would be too variable to be of value as an index of stock size owing to the highly variable nature of larval mortality rates.[2] In our study, we developed an age-adjusted larval index for king mackerel and evaluated the appropriateness of using larval indices in calibrating the king mackerel VPA.

Materials and methods

King mackerel larvae in the Gulf of Mexico have been collected annually since 1982 during Southeast Area Monitoring and Assessment Program (SEAMAP) ichthyoplankton surveys conducted by the states of Florida, Alabama, Mississippi, Louisiana, and by the National Marine Fisheries Service. Larvae were captured in oblique tows from near bottom to the surface with a 61-cm, 0.333-mm-mesh bongo net by following standardized SEAMAP collection procedures (Richards et al., 1993). Survey stations were typically located 55.56 km apart in a fixed grid, and sampled at all times of day or night. Collections were taken west of 88°W longitude in June and July from 1982 to 1985. Starting in 1986, gulf-wide samples were also collected in late August, September, and early October. Catches of king mackerel larvae were standardized to account for sampling effort and expressed as number of larvae under 10 m^2 of sea surface (no./10 m^2). Annual mean abundances, i.e. the indices not adjusted for age composition of larval catches, were based on arithmetic means. Use of the delta-distribution (Pennington, 1983) did not lower estimates of standard error.

The age composition of king mackerel larvae captured at each station was estimated by converting lengths to ages with a least squares regression model based on the length and age of larvae (n=47) collected in September 1986 from the Gulf of Mexico and Atlantic Ocean and aged by counting otolith growth increments[3] (DeVries et al., 1990). Two additional techniques for assigning larval ages from lengths were considered, namely a probability age-classification matrix (Scott, et al., 1993) and discriminant analysis, but these were found to be ineffective owing to the small number of aged larvae. Once ages were assigned, individual catch curves for each year of the time series from 1982 to 1995 were constructed from the descending arm of $\log_e$-transformed catch-at-age data (Ricker, 1975) by using the regression procedure of SAS (SAS Institute Inc., 1990). A dummy-variable model was used in the regression procedure to fit a single model for all years with test statements that tested for homogeneity of intercepts and of slopes. Instantaneous daily mortality rates and an age-adjusted index of abundance were then calculated.

The age-adjusted index for king mackerel was based on the abundance of a single age class to eliminate the influence of variable larval age composition among years. We arbitrarily chose one-day-old larvae as the standard age class on which to base the age-adjusted index. We estimated the density of one-day-old larvae at each station by back-calculating and summing their numbers from older age classes using an estimate of daily instantaneous mortality rate. The density of one-day-old king mackerel larvae at each station was estimated as

$$I_{y,s} = \sum_{i=1}^{k} N_{y,s,i} e^{Z(i-1)},$$

where $I_{y,s}$ = the number of one-day-old larvae under 10 m^2 of sea surface (y=year; s=station); and
$N_{y,s,i}$ = the number of larvae under 10 m^2 of sea surface of each age class represented in the sample (i=age class).

Annual mean age-adjusted index of larval abundance was estimated as the average of station values.

Annual estimates of spawning stock size (ages 1 through 11+ years) were obtained from a VPA of king mackerel.[4] No king mackerel larval occurrence data from SEAMAP were used to tune this VPA. However, the VPA used for the most recent stock assessment was calibrated with larval occurrence data. Residual plots from regressions between the VPA estimate of stock size indices of larval abundance exhibited no particular pattern; therefore data were not transformed for correlation analyses. Correlation between the VPA estimate of spawning stock size and three SEAMAP larval indices were then estimated by using the correlation procedure of SAS (SAS Institute Inc., 1990). Larval indices used were 1) frequency of occurrence; 2) mean abundance of all larvae captured unadjusted for age; and 3) mean abundance of age one-day larvae.

Results

The SEAMAP survey king mackerel larval frequency of occurrence index ranged from 0.02 (SE=0.017, CV=100%) in 1983 to 0.32 (SE=0.038, CV=12%) in 1995 (Table 1). The survey larval abundance index (no./10 m^2) ranged from 0.23 (SE=0.228, CV=100%) in 1983 to 5.15 (SE=0.924; CV=18%) in 1995 (Table 1). Mean frequency of occurrence and abundance of king mackerel larvae varied more during the first four years of the time series when observations were available from only the early part of the spawning season, i.e. summer months. However, both frequency of occurrence and abundance have increased over

[2] Powers, J. E. 1996. Personal commun. Southeast Fisheries Science Center, Miami Laboratory, Miami, FL 33149.

[3] DeVries, D. 1996. Personal commun. Southeast Fisheries Science Center, Panama City Laboratory, Panama City, FL 32407.

[4] Legault, C. 1998. Personal commun. Southeast Fisheries Science Center, Miami Laboratory, Miami, FL 33149.

the fourteen-year time series (Fig. 1A, Table 1). Variability decreased after 1986, when the fall SEAMAP ichthyoplankton survey was added which both extended coverage into the time period of peak king mackerel spawning and increased the number of samples. Coefficients of variation (100 × SE/mean) have been less than 20% for both frequency of larval occurrence (1989–95) and larval abundance (1992–95) for the most recent years of the time series (Table 1). Also an expansion in the areal distribution of king mackerel larvae has been apparent since 1986 (Fig. 2).

A total of 798 king mackerel larvae ranging in length from 1.6 to 10.1 mm were collected from 1982 to 1995 (Table 2). A quadratic equation best described the relationship between larval king mackerel age and length data (Fig. 3). Catch-at-age was calculated from the estimates of larval density and age frequencies and then used to construct annual catch-at-age curves for survey-captured king mackerel larvae. Over the time series, larvae ranged in age from 2 to 11 days, and estimates of instantaneous daily mortality rates for individual years ranged from 0.35 in 1985 to 0.70 in 1992 (Table 3). A single catch-at-age regression for all years combined indicated no significant difference among slopes (i.e. instantaneous mortality rates) or among intercepts. Therefore, a pooled regression model was fitted. The slope of the pooled regression gave an estimate of instantaneous daily mortality rate (Z) of 0.53 (Table 3) and was subsequently used to backcalculate the abundance of one-day-old larvae and generate the age-adjusted index of king mackerel larval abundance.

VPA estimates of king mackerel spawning stock size ranged from 46.03×10^5 individuals in 1985 to 101.93×10^5 individuals in 1995 (Fig. 1A). Survey larval frequency of occurrence and estimates of stock size corresponded with a correlation of 0.82 over the entire time series, 1982–95, and 0.92 for the period 1986–95 (Fig. 1A). The king mackerel survey index of larval abundance (unadjusted for age) was also highly correlated with spawning stock size (Fig. 1A). The correlation, 0.84, was the same for both periods of comparison, all survey years, and years since 1986. Our attempt to adjust larval abundance for age did not improve the correlation between the abundance index and spawning stock size. The correlation with spawning stock size was, however, higher after fall surveys began, 0.78 versus 0.65, but these values were both lower than those for the "uncorrected" abundance index and the index based on frequency of occurrence (Fig. 1B).

Discussion

Hunter and Lo (1993) asserted that fish eggs and larvae can be used not only to estimate the biomass of a fish stock but also to monitor trends in relative stock abundance. Indices of relative abundance are less costly to produce than biomass estimates from ichthyoplankton data, but they are also less precise. The CVs of the most precise biomass estimates based on ichthyoplankton data range between 20% and 30%. Whether adjusted for growth and mortality of larvae or not, ichthyoplankton indices are "surprisingly sensitive to major changes in stock abundance" (Hunter and Lo, 1993). It should be of no surprise that our indices based on abundance and frequency of occurrence of king mackerel larvae from SEAMAP collections in the Gulf of Mexico closely tracked trends in adult abundance over the time

Table 1

SEAMAP annual estimates of king mackerel larval mean abundance and frequency of occurrence (n=number of stations, CV=100×SE/mean).

		Number/10 m^2			Frequency of occurrence		
Year	n	Mean	SE	CV (%)	Mean	SE	CV (%)
1982	77	0.83	0.464	56	0.09	0.033	36
1983	59	0.23	0.228	100	0.02	0.017	100
1984	74	1.19	0.413	35	0.18	0.045	25
1985	94	0.36	0.178	49	0.06	0.025	40
1986	225	1.10	0.286	26	0.10	0.020	20
1987	216	0.69	0.161	23	0.12	0.022	19
1988	125	0.97	0.319	33	0.11	0.028	25
1989	129	2.08	0.714	34	0.19	0.034	18
1990	129	1.67	0.357	21	0.21	0.036	17
1991	129	1.33	0.368	28	0.18	0.034	19
1992	167	2.00	0.338	17	0.28	0.035	12
1993	175	3.22	0.546	17	0.30	0.035	12
1994	176	2.82	0.503	18	0.26	0.033	13
1995	155	5.15	0.924	18	0.32	0.038	12

series. Annual estimates of mean king mackerel occurrence were more precise than the estimates of larval abundance, and CV's for both king mackerel indices were comparable to CVs of ichthyoplankton-based estimates for other species (Hunter and Lo, 1993). Larval abundance of Atlantic bluefin tuna, a species that poses a more intractable sampling problem than does king mackerel, namely an immense spawning area (the open Gulf) and lower overall abundance, has been used as a tuning variable in population assessments by VPA (Scott et al., 1993).

The use of a simple larval index for monitoring stock size is not unprecedented. Data from larval surveys of Atlantic herring (*Clupea harengus harengus*) in the North Sea have been used since 1967 as the sole source of information on stock size or in combination with catch statistics or acoustic surveys, or both (Heath, 1993). One of the two larval indices for North Sea herring, the larval abundance index, employs only larvae less than 10 mm in length (up to 15 days old). The correlation between this larval index and stock size became weaker with increasing age of larvae owing, it was surmised, to interannual variation in mortality and dispersal. The potential influence of varying mortality rates and dispersal were likewise minimized in our study because most king mackerel larvae collected during the SEAMAP surveys were less than 5 mm and no more than ten days old. The other larval herring abundance index for the North Sea, the larval production estimate, utilizes all size and age groups to estimate the abundance at hatching and requires estimates of growth and mortality rates. Both herring indices are calculated annually; however, the actual use of each in VPA assessment is dependent on survey coverage in time and space in relation to spawning events for that year.

Our attempt to account for differences in larval age composition among years by adjusting the index for mortality of larvae did not improve the correlation with stock size. There are a number of reasons for this outcome. It is very likely that the limited age-at-length data available for conversion of king mackerel lengths to age probably resulted in imprecise assignment of ages. Overestimation of age by a single day would result in a 70% error in the backcalculated abundance of age one-day fish, and a 41% error if underestimated. Hauser and Sissenwine (1991) noted that estimates of larval production using "back-calculation techniques," as we did to estimate the abundance of one-day-old king mackerel larvae, will be biased if the growth rate used is incorrect or if mortality is size dependent, or both conditions transpire. It is also likely that the assumption of constant mortality rate, an integral part of catch curve analysis, did not hold for king mackerel larvae. Bailey et al. (1996a; 1996b) found that early mortality rates of walleye pollack larvae were not only highly variable among years but declined as larvae became older. Furthermore, the observation that instantaneous mortality rates of king mackerel larvae among years were not significantly different may be caused by the low number of larvae caught and the small number of age classes represented in collections (Comyns, 1997). However, an age-adjusted index calculated with annual estimates of mortality rate had a much poorer correlation with stock size; therefore we did not report these data. Our estimate of mortality (Z=0.53) may be biased high owing to net selectivity, i.e. avoidance of the net by larger larvae. To correct this bias, we truncated the upper 20% of the size distribution and recalculated mortality rates and an age-adjusted index. Although the mortality estimate was lower (Z=0.43), the correlation between stock size and the age-adjusted index based on this mortality rate did not differ from the correlations based on nontruncated distributions.

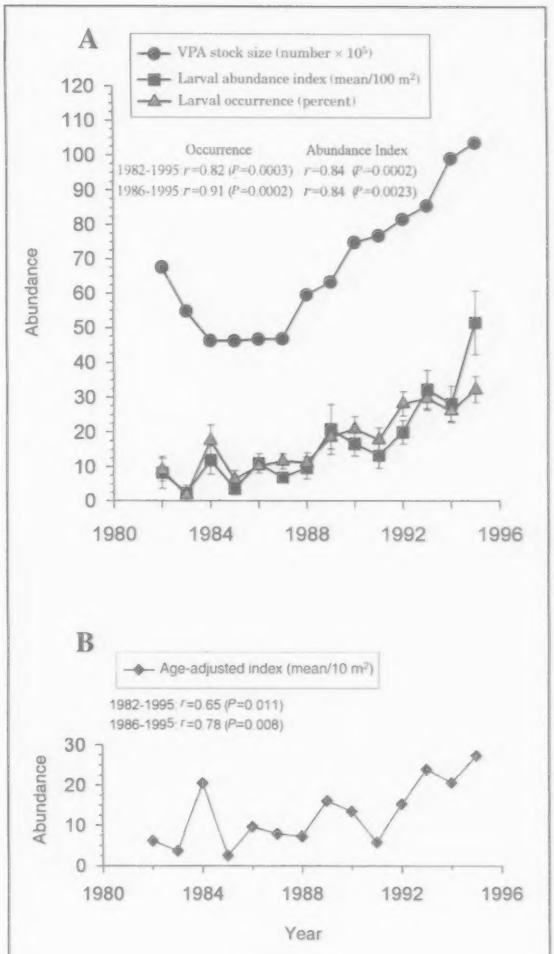

Figure 1

(**A**) King mackerel adult spawning stock size (number × 10^5 of fish in the 1 through 11+ age groups) estimated by VPA, survey larval index of abundance (mean number under 100 m² of sea surface ±SE), and survey larval frequency of occurrence (percent of stations where larvae were captured ±SE). (**B**) Annual age-adjusted larval index of abundance (mean number under 10 m² of sea surface).

Another measure of king mackerel stock size was considered, namely the VPA-generated estimate of egg pro-

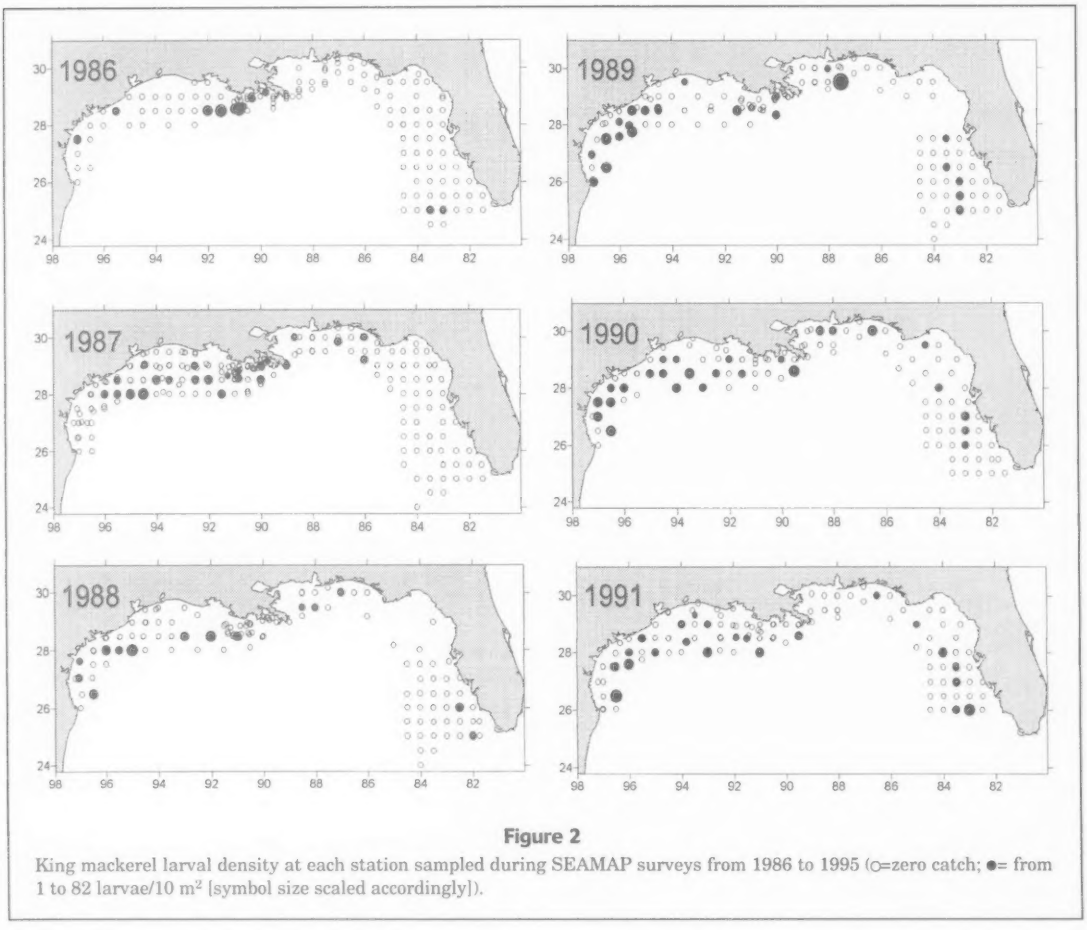

Figure 2

King mackerel larval density at each station sampled during SEAMAP surveys from 1986 to 1995 (○=zero catch; ●= from 1 to 82 larvae/10 m^2 [symbol size scaled accordingly]).

duction (number-at-age × relative fecundity-at-age). This measure accounts for the presumably greater contribution of older and larger fish to overall reproductive output; therefore it would seem a better correlate of larval occurrence and abundance than numbers of fish. However, we found egg production to be somewhat less correlated with larval indices than were numbers of fish, perhaps owing to the use of a constant fecundity-at-age distribution to estimate king mackerel egg production. Significant interannual differences in relative fecundity have been demonstrated for a wide variety of fishes (Bagenal, 1966; 1967; Bagenal and Braum, 1971; Hunter et al., 1985; Rijnsdorp, 1991; Koslow et al., 1995). But there is insufficient data on fecundity of king mackerel over the time series to ascertain the influence of interannual variability on this parameter, and in turn, on larval production.

Application of growth and mortality rates to refine or adjust larval indices of relative abundance may be moot because determinants of larval survival, i.e. predation or starvation rates, or both, appear to be unrelated to spawning stock abundance (Hunter and Lo, 1993). It has been argued that larval occurrence provides a more useful index of stock size because stock size and the geographic area occupied by eggs and larvae may be correlated, as is the case for Pacific sardines (*Sardinops sagax*) and northern anchovy (*Engraulis mordax*), especially at low population levels. (Mangel and Smith, 1990; Smith, 1993; Hunter and Lo, 1993; MacCall, 1988). However, Mangel and Smith (1990) suggest that a switch from presence and absence data to actual counts would be necessary when the spawning biomass increases to a level where "virtually all stations have eggs."

King mackerel in the Gulf of Mexico are rebounding from the low levels of the late 1970s and early 1980s (Powers and Restrepo, 1993), and the increases are reflected in larval occurrence and abundance. A switch to a larval abundance index may be required to follow trends in stock size as larval abundance rises if the uncorrected abundance index at some future time no longer corresponds to stock size. Adjustment of the king mackerel larval abundance index would require annual estimates of mortality and growth rates by direct aging of survey-caught larvae. For now, both the index of larval occurrence and the unadjusted index of abundance from SEAMAP collec-

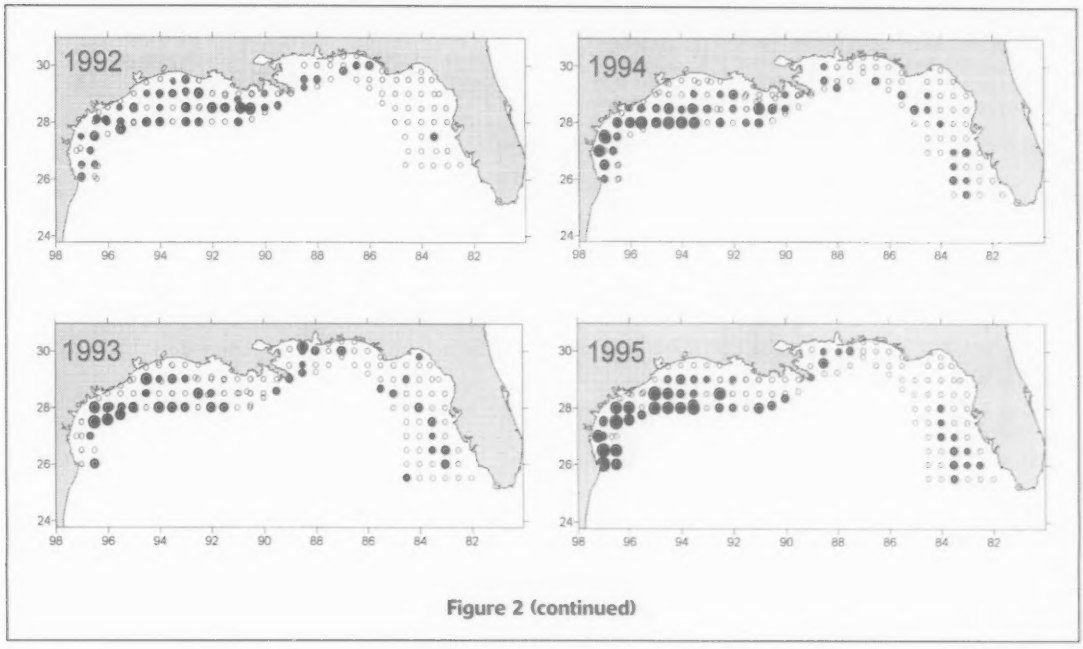

Figure 2 (continued)

Table 2

Average length (mm) and age (days) of king mackerel larvae collected during annual surveys (*n*=number of larvae measured).

		Length				Age			
Year	*n*	Mean	SE	Min	Max	Mean	SE	Min	Max
1982	29	3.4	0.231	2.0	6.0	4.47	0.257	2.81	7.25
1983	4	4.9	0.860	4.0	7.5	6.08	0.880	5.13	8.71
1984	20	4.7	0.467	2.2	8.7	5.84	0.494	3.05	9.81
1985	12	3.8	0.330	1.9	5.5	4.89	0.369	2.69	6.74
1986	63	3.9	0.170	1.8	8.0	4.94	0.183	2.57	9.18
1987	35	4.3	0.267	1.9	7.5	5.39	0.297	2.69	8.71
1988	28	3.6	0.245	2.0	6.8	4.62	0.270	2.81	8.04
1989	58	3.5	0.171	2.0	10.0	4.53	0.182	2.81	10.91
1990	49	3.6	0.232	1.6	9.8	4.64	0.249	2.32	10.74
1991	33	3.1	0.209	1.8	6.0	4.06	0.236	2.57	7.24
1992	86	3.3	0.157	1.7	8.5	4.28	0.171	2.45	9.63
1993	137	3.3	0.133	1.7	10.1	4.27	0.142	2.45	10.99
1994	105	3.4	0.164	1.8	9.6	4.35	0.177	2.57	10.58
1995	139	3.2	0.100	1.8	8.1	4.18	0.111	2.57	9.27

tions reflect trends in spawning stock size and provide useful variables for calibrating the king mackerel VPA.

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Table 3

Individual annual and pooled catch curve parameters. ($\log_e$(number) = $\beta_0 + \beta_1$ *Age*; *n*=number of age groups.)

Year	*n*	β_0	β_1	r^2
1982	4	0.323	–0.444	0.86
1983	2	0.063	–0.366	1.00
1984	4	1.657	–0.505	0.51
1985	3	–0.824	–0.345	0.09
1986	7	1.343	–0.638	0.83
1987	5	–0.032	–0.431	0.41
1988	6	–0.631	–0.557	0.82
1989	5	1.638	–0.629	0.67
1990	7	1.642	–0.654	0.88
1991	6	0.643	–0.573	0.63
1992	7	1.757	–0.700	0.71
1993	8	1.485	–0.509	0.94
1994	8	1.332	–0.574	0.91
1995	7	2.187	–0.636	0.84
Pooled (1982–1995)	78	0.940	–0.529	0.65

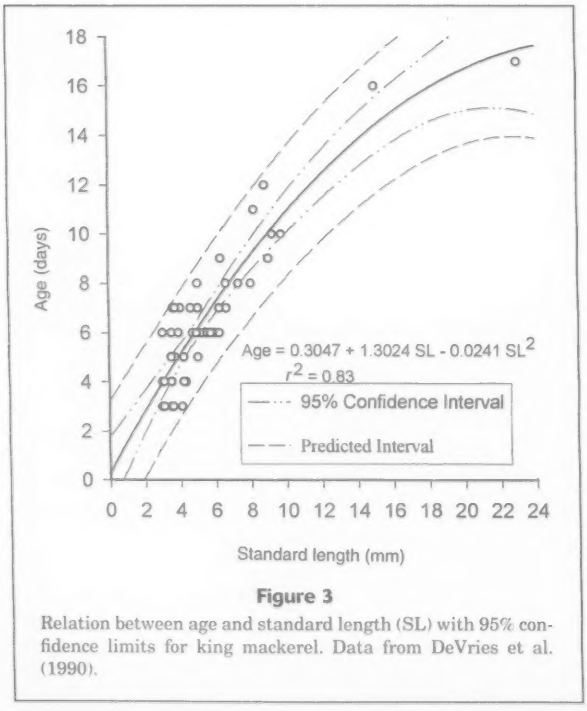

Figure 3

Relation between age and standard length (SL) with 95% confidence limits for king mackerel. Data from DeVries et al. (1990).

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Evasive behavior of spotted and spinner dolphins (*Stenella attenuata* and *S. longirostris*) during fishing for yellowfin tuna (*Thunnus albacares*) in the eastern Pacific Ocean

Gisela Heckel
Facultad de Ciencias Marinas
Universidad Autónoma de Baja California
Plácido Mata 2309 Depto. D-5
Condominio Las Fincas
22820 Ensenada
Baja California, México
E-mail address: gheckel@telnor.net

Kim E. Murphy
Facultad de Ciencias Marinas
Universidad Autónoma de Baja California
Km 103 Carretera Tijuana-Ensenada
22800 Ensenada,
Baja California, México

Guillermo A. Compeán Jiménez
Programa Nacional de Aprovechamiento del Atún y de Protección de Delfines
Km 107 Carretera Tijuana-Ensenada
Campus CICESE
22800 Ensenada
Baja California, México

Abstract—This study examines the question of whether the evasive behavior of northeastern offshore spotted dolphins (*Stenella attenuata*) during fishing for tuna (by the Mexican fleet) varies in geographic areas of the eastern Pacific Ocean (EPO). It also investigates whether evasion differs between northeastern offshore spotted and eastern spinner dolphins (*Stenella longirostris orientalis*). Observations recorded in the database of the Mexican Programa Nacional de Aprovechamiento del Atún y de Protección de Delfines (PNAAPD) from 1992 to 1995 were analyzed. The calculated evasion index was the estimated percentage of dolphins that evaded capture in relation to the herd's estimated initial size in each set.

Evasion index by set was averaged in 2×2 quadrants and then used to draw a contour map. Three areas were outlined with low (25%), medium (44.44%), and high (71.80%) median evasion indices. These areas were significantly different ($P<0.0001$) according to the Kruskal-Wallis nonparametric multisample test, thus indicating a spatial pattern in evasive behavior of northeastern offshore spotted dolphins during fishing operations of the Mexican fleet. Spatial patterns in evasive behavior might be related to the dolphins' learning capacity, hence experience of individual dolphins or herds with tuna purse-seining in the EPO should be estimated to demonstrate this. To be representative, future research should utilize available historical fishing effort data for the international fleet. Furthermore, a multivariate approach to this issue is necessary.

One of the investigated areas (mouth of the Gulf of California) was further analyzed regarding differences between two stocks of dolphins. Evasion indices for eastern spinners were significantly different from those for northeastern offshore spotted dolphins ($P<0.0001$, Kolmogorov-Smirnov two-sample test). This difference may correspond to different evasive strategies used by the two stocks to evade capture in the net, such as evasion under the net and dispersion (division of herd into subgroups during the set). Eastern spinners apparently evaded more frequently than northeastern offshore spotted dolphins by diving under the net. During the three set stages of tuna fishing (before chase, during chase, and during encirclement), eastern spinner dolphins dispersed less often than spotted dolphins, behavior that may permit them to coordinate their evasive movements more effectively than northeastern offshore spotted dolphins. Evasion over the net was rarely observed in either stock.

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The tuna fishery in the eastern Pacific Ocean (EPO) sets purse seines in three major modes: school, log, and dolphin fishing. Yellowfin tuna (*Thunnus albacares*) and certain species of dolphins are found to associate in the EPO. The spotted dolphin (*Stenella attenuata*) is by far the most important species from the point of view of its frequency of association with tuna and its use by fishermen for catching tuna (Perrin, 1969). The frequent appearance of spinner dolphins (*Stenella longirostris*) in sets also makes this species significant, although in almost all cases it appears in mixed herds with the spotted dolphin (National Research Council, 1992).

During "dolphin fishing" or "fishing on dolphins," the net is set around the tuna and the dolphins after a period of chase. Once a dolphin herd is sighted with high-power binoculars (25×), four to six speedboats are lowered, and the chase begins. The speedboats herd the dolphins and the accompanying tuna into a tight group that can be encircled by the seiner. The dolphins may try to evade the boats to avoid capture. Those that do not succeed are released by the fishing crew during the "backdown" procedure (a procedure in which the vessel is run in reverse to pull the corkline underwater and thus release the dolphins) (Barham et al., 1977).

Impact of the fishery on cetacean populations has been assessed by estimating cetacean abundance and distribution involved in tuna purse-seining, as well as by estimating mortality rates. By 1988, the estimated abundance of the northeastern offshore spotted dolphin had been reduced to between 19% and 28% and that of the eastern spinner dolphin and to between 32% to 58%

in relation to estimated pre-exploitation levels (Wade, 1993; Wade[1]). Therefore, these stocks have been designated as depleted under the U.S. Marine Mammal Protection Act. However, when compared to abundance estimates from 1986–90 research surveys (Wade and Gerrodette, 1993), preliminary estimates from the most recent surveys (Gerrodette[2]) show a noticeable increase in the abundance of the northeastern offshore spotted and the eastern spinner dolphin compared to previous estimates (Wade and Gerrodette, 1993).

In addition to abundance estimation, the total incidental mortality (all species and stocks involved in the fishery and for the international fleet) was estimated at 3274 for 1995, which represents 0.03% of the total population (Hall and Lennert, 1997) of 9.6 million for all dolphin species involved in the tuna fishery (Wade and Gerodette, 1993). The Mexican Programa Nacional para el Aprovechamiento del Atún y de Protección de Delfines (PNAAPD) estimated the incidental mortality (of all species and stocks) of the Mexican fleet to be 1819 dolphins in 1994 (Compeán et al.[3]).

Important efforts have been aimed at reducing mortality rates, such as improving fishing gear (Barham et al., 1977; Coe et al., 1984), placing quotas on the number of dolphins killed for each stock (Wade[4]), placing a quota on the number of dolphins killed by fishing vessel and making the backdown procedure mandatory (Colson, 1992).

Other efforts in reducing mortality have been directed towards research on dolphin behavior during tuna purse-seining (Norris et al., 1978; Pryor and Kang[5]). Mortality rates may also be reduced by understanding more about the dolphins' behavior, so that they are less likely to injure themselves or die during fishing practices (Norris et al., 1978).

Some research indicates that some dolphin stocks may have reduced mortality through behavioral adaptations. The first ethological research on *Stenella attenuata* and *Stenella longirostris* during fishing operations was accomplished by Norris et al. (1978). They focused on overall herd movements and interanimal distances and developed the first ethogram for these animals during a net set for tuna. Pryor and Kang (1980) also made observations during seining operations but focused more on individual and subgroup behavior. Although Norris et al. (1978) described high stress levels in dolphins that were involved in sets, Pryor and Kang interpreted their own data as indicating much learned adaptive behavior and low stress levels. By analyzing records from observers on tuna boats, Stuntz and Perrin[6] noted and discussed the fact that dolphins (*Stenella* spp.) were more difficult to capture in areas where fishing effort had been higher and the authors concluded that dolphins had been able to learn to evade capture from tuna boats.

Data collected by observers on board tuna purse-seiners from 1992 to 1995 (PNAAPD database) were used to investigate whether the evasive behavior[7] of northeastern offshore spotted dolphins (*Stenella attenuata*) during fishing for yellowfin tuna varied geographically in the EPO. Differences in evasive behavior between the northeastern offshore spotted and the eastern spinner dolphin (*Stenella longirostris orientalis*) were also assessed. Furthermore, differences in evasive strategies[8] between these two stocks were described.

Methods

Data collection

Data from 1992 to 1995 from the PNAAPD database (Mexican fleet) were used to study evasive behavior of two stocks of different species in the EPO: the northeastern offshore spotted dolphin, a stock of the pantropical spotted dolphin (*Stenella attenuata*), and the eastern spinner dolphin (*Stenella longirostris orientalis*), a subspecies and stock of the spinner dolphin (*Stenella longirostris*) (Dizon et al., 1994; Perrin and Gilpatrick, 1994; Perrin et al., 1994).

Observers (also referred to as scientific technicians) from the Inter-American Tropical Tuna Commission (IATTC)

[1] Wade, P. R. 1993. Estimation of historical population size of the northeastern stock of offshore spotted dolphin (*Stenella attenuata*). Southwest Fisheries Science Center Administrative Report LJ-93-18, 18 p. Southwest Fisheries Science Center, Natl. Mar. Fish. Serv., NOAA, 8604 La Jolla Shores Drive, La Jolla, CA 92038-0271.

[2] Gerrodette, T. 1999. Preliminary estimates of 1998 abundance of four dolphin stocks in the Eastern Tropical Pacific. http://swfsc.ucsd.edu/IDCPA/Abund98.html. Southwest Fisheries Science Center., Natl. Mar. Fish. Serv., NOAA, P.O. Box 271. La Jolla, CA 92038

[3] Compeán J., G. A., I. Méndez G.-H. and I. Méndez R. In preparation. Annual estimates of incidental mortality for dolphin species associated with the Mexican tuna fishery during 1992–1995. Programa Nacional para el Aprovechamiento del Atún y de Protección de Delfines (PNAAPD). Km 107 Carretera Tijuana-Ensenada, Campus CICESE, 22800 Ensenada, B.C., México.

[4] Wade, P. R. 1993. Revised estimates of fisheries kill of dolphin stocks in the eastern tropical Pacific, 1959–1972. Southwest Fisheries Science Center Administrative Report LJ-93-17, 19 p. Southwest Fisheries Science Center, Natl. Mar. Fish. Serv., NOAA, 8604 La Jolla Shores Dr., La Jolla, CA 92038-0271.

[5] Pryor, K., and I. Kang. 1980. Social behavior and school structure in pelagic porpoises (*Stenella attenuata* and *S. longirostris*) during purse seining for tuna. Southwest Fisheries Center. Admin. Rep. LJ-80-11C. Southwest Fisheries Science Center, 8604 La Jolla, Shores Drive, La Jolla, CA 92038-0271.

[6] Stuntz, W. E., and W. F. Perrin. 1979. Learned evasive behavior by dolphins involved in the eastern tropical Pacific tuna purse seine fishery. Unpubl. abstract. Third Biennial Conference on the Biology of Marine Mammals, October 7–11, 1979, Seattle, WA.

[7] Evasive behavior: In this study, calculated as a percentage of the estimated number of dolphins that avoided capture in the net relative to the best estimate of the initial herd size (before the set started) by the observer or scientific technician. See "Methods" section.

[8] Evasive strategies: movements of the herd or subgroups of dolphins in relation to seiner, speedboats, and net (when it has been set and before rings up) by which dolphins attempt to avoid capture in the net.

and corresponding national programs have worked on board tuna vessels. Since 1991, the PNAAPD has placed observers on board 50% of the trips by Mexican tuna boats (the remaining 50% is covered by IATTC observers). Observers record data during dolphin sets, using standardized data forms and instructions provided by the PNAAPD (which are very similar to those used by the IATTC). A detailed description of data collection and procedures can be found in Perrin et al. (1983) and Polachek.[9] In summary, in the "Daily Activity Record" (DAR), observers keep a daily log on events (date, time of day, departure, arrival, sightings, sets, geographic position, aerial assistance during a set, etc.), weather conditions (cloud cover, sea state, visibility, water temperature), and tuna catch. In other forms they also record the vessel's features and all data concerning marine mammal sightings and sets, school and log sets, sea turtle sightings, and more recently, bycatch.

When a marine mammal group is sighted (which might lead to a net set for tuna catch), observers fill out the "Record of Marine Mammal Observations and Set Data" (RMMOSD). Herd size and composition (percent and species or stock identification) is annotated as estimated by the observer (usually with 7×50 or 10×50 binoculars), a crew member on board (with 20× or 25× binoculars), and another crew member from the helicopter. At the end of a set, the observer has to decide on his "best estimate" of the herd size and composition before the actual set occurred. During a set, the observer estimates the number of dolphins (identified by species or stock) that actively evade the boats and net before the chase, during the chase, and during the encirclement, as well as the number of groups within the herd during each of the three set stages. The number of dolphins deliberately cut out by the skipper, those that evade by diving under the net or escape by leaping out of the net are also estimated and identified by the observer All these data were of interest for our study (except dolphins deliberately cut out because this action was not considered evasion actively achieved by dolphins). Other data recorded by the observer are chase and set times, number of speedboats used, whether or not explosives were used, the number and composition of captured marine mammals (those that were encircled), number of animals rescued and the manner of their rescue, start and end of backdown, number of dolphins hurt or killed, and further details about the fishing procedure.

The observers' estimates of herd size and number of dolphins evading capture may be biased owing to differing experience and estimation between observers. However, they attend a complete training course at the institution they work for (IATTC, PNAAPD, or other national programs), where they learn to identify fauna species they may encounter at sea (marine mammals, fish, birds, and sea turtles), how the fishing operation proceeds, and how to collect data. At the end of each trip, experienced editors at the institutions review the observers' collection of data. These procedures give credence to the data collected. Moreover, reactions of dolphins to approaching survey vessels have been studied previously by means of field experiments (Au and Perryman, 1982; Hewitt, 1985). Their results might be compared to the dolphins' behavior "before chase" because sighting distance in those studies (as during the fishing operation) was usually between 2 and 6 or 7 nmi (nautical miles), aided with 20× or 25× binoculars. Dolphins started to react (by changing their swimming speed and course) between 1.5 to 3 nmi distance to the ship (Hewitt, 1985) with one exception, where the herd reacted at 6 nmi (Au and Perryman, 1982). Almost half of the herds observed by Hewitt (1985) did not react at all. Therefore, the observer's estimate of initial herd size (which is also compared to the estimate by a crew member on board and by the crew member in the helicopter) was assumed to be reliable. We also relied on the observer's estimation of number of dolphins evading capture during all set stages (before chase, during chase, and during encirclement) because of their training and experience.

The logbooks with these observations are collected by the institution for which the observer works. To improve the accuracy and reliability of the observers' records, careful debriefing and editing is accomplished by skilled technicians (with considerable experience at sea) at the institutions (in our study, the PNAAPD). The observations are then entered into the corresponding computerized databases which are also checked for errors that might have occurred during "capture" (entry) of the data into the database (Perrin et al., 1983; Polacheck[9]).

Confidence in the databases of the IATTC and national programmes (PNAAPD and the U.S National Marine Fisheries Service) is acknowledged with the publication of studies that have analyzed some of these data. A few examples of such studies are the following: dolphin distribution (Perrin et al., 1983; Perrin et al., 1985), dolphin abundance estimation (Anganuzzi et al., 1992; Polachek[9]), incidental kill of dolphins in tuna fishing nets (Hall and Lennert, 1997; Wade[4]), dolphin life history (Chivers and De Master, 1994), tuna-dolphin association (Edwards, 1992; Scott and Cattanach, 1998), blue whale distribution in the eastern tropical Pacific (Reilly and Thayer, 1990), and aspects of the Mexican tuna fishery (Compeán and Dreyfus, 1996).

In our study, spatial patterns in evasive behavior of the northeastern offshore spotted dolphin were described, as well as differences in evasive behavior and strategies (herd dispersion,[10] evasion under and over the net) between

[9] Polachek, T. 1984. Documentation of the time sequential file created from the tuna boat observer data bases for analyzing the relative abundance of dolphins in the eastern tropical Pacific. Southwest Fisheries Science Center Admin. Report LJ-84-33, 26 p. National Marine Fisheries Service.

[10] Herd dispersion: to establish if a herd dispersed during a set, the grouping codes applied by the observers in paragraph 3 of the RMMOSD were used. The codes are the following: 1, herd is in one group; 2, herd has divided into two or three groups; 3, herd consists of more than three groups. These codes are recorded during three set stages: before chase, during chase, and during encirclement. For each species, the number of sets where the specified grouping code occurred was counted during each set stage. If codes were in ascending order, this was interpreted as herd dispersion during the fishing operation.

the northeastern offshore spotted and the eastern spinner dolphin (*Stenella longirostris orientalis*). A subset of the PNAAPD database (1992–95) was extracted from sections of the DAR (those referring to date and set position) and the RMMOSD (observer's best estimation of herd size and composition by species and stock, number and identification [also by species and stock] of evading and escaping dolphins, as described previously), and grouping codes. Data from sets that were interrupted (due to loss of tuna catch because all dolphins escaped from the chase or mechanical problems of the vessel or net performance, etc.) were excluded from the analyses.

Because data collected by the Mexican observer program (PNAAPD) represented 50% of the Mexican fleet's effort in the EPO, we assumed that the data set in our study was sufficiently large to represent the dolphins' evasive behavior in relation to Mexican tuna fishing boats during the sampled period.

Data analysis

Evasion index by set Evasion index by set was calculated in order to search for spatial patterns in evasive behavior of the northeastern offshore spotted dolphin and to analyze differences between northeastern offshore spotted and eastern spinner dolphins. This index is defined as the estimated percentage of dolphins that evaded capture during each set in relation to the herd's estimated initial size:

$$\hat{I}_{ij} = \left(\frac{\hat{E}}{\hat{H}}\right)100,$$

where $\hat{I}_{ij}$ = estimated evasion index during set i in quadrant j;
$\hat{E}$ = number of dolphins that evaded capture during set i in quadrant j, i.e. the sum of escaping dolphins estimated by the observer before the chase, during the chase, and during the encirclement as recorded in the RMMOSD;
$\hat{H}$ = herd size before chase started during set i in quadrant j, i.e. the observer's best estimate as recorded in the RMMOSD.

Evasion index by set was stratified by stock by selecting from the database only sets on pure herds (i.e. those herds composed 100% of a species) of northeastern offshore spotted dolphins and sets on pure herds of eastern spinner dolphins. Because only these two stocks were studied, results should not be considered representative of the corresponding species (pantropical spotted dolphin, *Stenella attenuata*, and spinner dolphin, *Stenella longirostris*).

Sets in which no dolphins escaped and therefore the calculated evasion index was zero were included in all analyses because they indicated that evasive behavior did not occur or failed. This action is contrary to common practice where "zeros" are often eliminated because they represent missing data that tend to bias calculations.

Spatial patterns in evasive behavior of northeastern offshore spotted dolphins To evaluate if there were spatial patterns in evasive behavior for the data in our study a computer program based on Matlab version 4.2c was used to plot the evasion index by set of the northeastern offshore spotted dolphin on a map of the EPO. The program calculated average evasion index by set in 2×2 quadrants to smooth the data which were then used to draw a contour map with the commercial surface mapping program Surfer version 6.01 (Smith et al., 1995). This software interpolated the average evasion index by set in 2×2 quadrants to form a regular rectangular array of grid values. This procedure was chosen because the smoothness of contours on a contour map is partially a function of the number of X and Y lines in the grid. When a grid is created, reducing the number of lines in the X and Y directions can result in more angular contours on the contour map. Most of the gridding methods in Surfer use a weighted average interpolation algorithm. The gridding method called "Kriging" with a linear variogram was chosen because it incorporates anisotropy and underlying trends in an efficient and natural manner and has been proven to be quite effective for many data sets in different fields (Smith et al., 1995).

A geographic difference in evasive behavior was observed in the contour map (see "Results" section, Fig. 1), and the 60%, 50%, and 40% contours were considered the limits between three areas with different evasive behavior (as defined by the evasion index) during the study period and for the Mexican fleet. In addition, the following statistical procedures were applied to test for significant differences in mean evasion indices of the three areas.

Analysis of variance (ANOVA) can be used to compare the mean of three groups of proportions (i.e. for each area) (Zar, 1999). Because proportions (like the evasion index) have a binomial distribution, the individual data should be transformed as follows in order to meet normality and homoscedasticity assumptions (Zar, 1999):

$$\hat{I}'_{ij} = 0.5\left(\arcsin\sqrt{\frac{\hat{E}}{\hat{H}+1}} + \arcsin\sqrt{\frac{\hat{E}+1}{\hat{H}+1}}\right),$$

where $\hat{I}'_{ij}$ = estimated transformed evasion index during set i in quadrant j;
$\hat{E}$ = estimated number of dolphins that evaded capture during set i in quadrant j; and
$\hat{H}$ = estimated herd size before chase during set i in quadrant j.

After transformation, the data still did not have a normal distribution (Kolmogorov-Smirnov goodness-of-fit test, D=0.0704, P<0.01, n=808; Zar, 1999). Therefore, distribution-free tests were used to search for significant differences between the three evasion areas (Conover, 1980; Neave and Worthington, 1988).

To search for significant differences between the medians (usual group average measure in nonparametric statistics) of three groups (evasion areas), the nonparametric Kruskal-Wallis multisample test seemed to be the most appropriate for the data in our study. The reasons for this

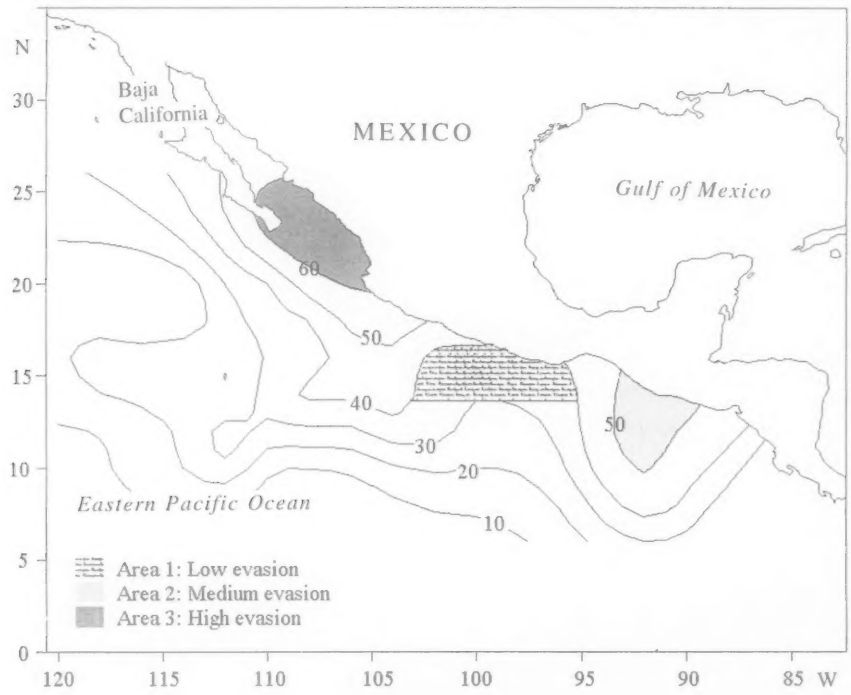

Figure 1

Estimated evasion index by set (estimated percentage of dolphins that evaded capture during each set in relation to estimated initial herd size) for northeastern offshore spotted dolphins (1992–95, Mexican fleet, PNAAPD data). Three areas were delimited according to 60%, 50%, and 40% evasion index contours.

are that data were measured in an interval scale (the test requires at least an ordinal scale), and samples are considered to be independent when it is assumed that dolphins remain approximately in the same area. Even though the swimming capacity of dolphins is well known, it is difficult to establish how fast or far they are able to travel. The Kruskal-Wallis test was preferred over the median test (with simpler calculations) because the latter uses the data more crudely than the former, and so the median test will generally be somewhat less powerful (Conover, 1980).

The Kruskal-Wallis test ranks all observations from 1 to n, and its statistic (H) is based on comparing each group's mean rank with the mean of all the ranks, weighted by the appropriate sample size to compensate for the effect of unequal sample sizes (Neave and Worthington, 1988). If the differences among the three evasion areas proved to be significant, nonparametric multiple comparisons could be executed to find which areas could be most confidently claimed to have different medians from each other (Conover, 1980; Neave and Worthington, 1988). The statistic for multisample comparisons (T) is obtained by calculating the absolute differences between the means of ranks assigned to the samples and then dividing these difference by their standard deviations. The T statistic has approximately the standard normal distribution; therefore H_0 will be rejected if $T>z$ (Conover, 1980; Neave and Worthington, 1988). Statistical procedures were performed with computing packages Statistica version 4.2 (StatSoft, 1993) and BMDP (Dixon, 1990).

Differences between stocks To evaluate differences in evasive behavior between eastern spinner and northeastern offshore spotted dolphins, estimated evasion indices by set for both stocks in evasion area 3 (as outlined in Fig. 1) were compared. Areas 1 and 2 were excluded from the analysis because eastern spinner sample sizes were smaller than 30 and these sizes were considered insufficient for statistical analysis when compared to sample sizes in area 3. Northeastern offshore spotted data were not normally distributed, and nonparametric tests were again used to compare the two independent samples (two stocks).

To decide which test was the most appropriate, "box-and-whisker" plots (Du Toit et al., 1986) were drawn to look for general distribution similarities or differences between both data sets (Fig. 2). The apparent difference in the medians would be worthwhile testing with the Mann-Whitney two-sample test (Conover, 1980; Neave and Worthington, 1988). However, data sets seemed to be different in spread (Mann-Whitney assumes equal spread); therefore a more

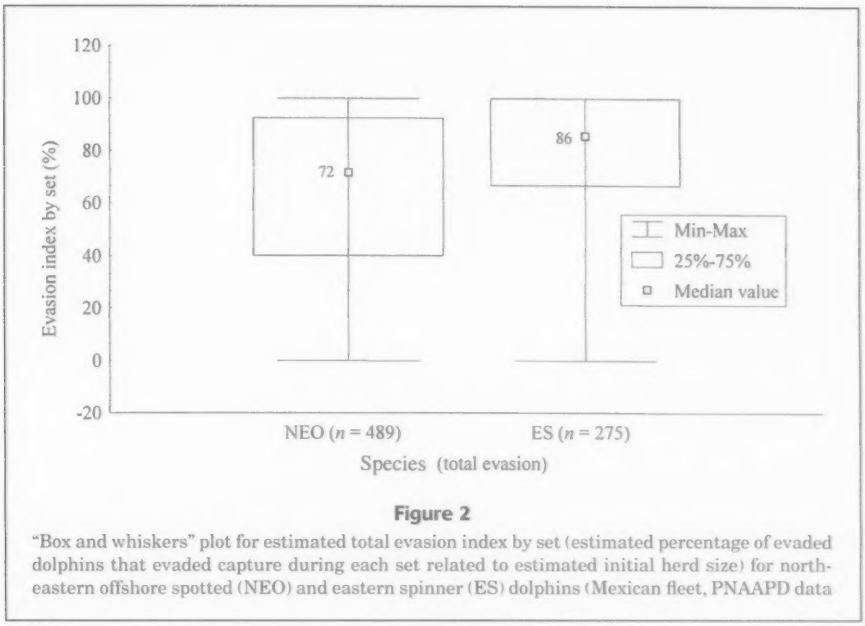

Figure 2

"Box and whiskers" plot for estimated total evasion index by set (estimated percentage of evaded dolphins that evaded capture during each set related to estimated initial herd size) for northeastern offshore spotted (NEO) and eastern spinner (ES) dolphins (Mexican fleet, PNAAPD data

cautious approach would be to apply the nonparametric Kolmogorov-Smirnov two-sample test because differences in location (average) and spread are tested simultaneously (Conover, 1980; Neave and Worthington, 1988). The Kolmogorov-Smirnov test compares the cumulative distribution function of two samples and uses the maximum vertical difference between them as the test statistic D (Neave and Worthington, 1988).

Eastern spinner and northeastern offshore spotted dolphins were also compared with respect to the dolphins' evasive strategies, such as evasion under and evasion over the net. The Kolmogorov-Smirnov test for two independent samples was used to evaluate estimated evasion indices by set between the stocks when they evaded capture by swimming under the net. The one-sided test was used to confirm if the evasion indices by set in one stock were larger than in the other. Differences in estimated evasion indices by set, when dophins evaded capture by swimming over the net, were not tested owing to very low sample sizes (n=3 in the northeastern offshore spotted, n=5 in the eastern spinner dolphin).

Furthermore, differences between the two stocks were described with respect to the dolphins' dispersion, i.e. the ability of the herds to "explode" (separate suddenly) (Allen et al., 1980) into subgroups in relation to the herds' configuration before the chase. For this description, the grouping codes applied by the observers in paragraph 3 of the RMMOSD were used. The codes used were the following: 1, herd is in one group; 2, herd has divided into two or three groups; 3, herd consists of more than three groups. These codes were recorded during three set stages: before chase, during chase, and during encirclement. For each stock, the number of sets where the specified grouping code occurred was counted during each set stage. If codes were found in ascending order, this was interpreted as herd dispersion during the fishing operation.

To test for significant differences in dispersion behavior between northeastern offshore spotted and eastern spinner dolphins, only data for evasion area 3 (Fig. 1) were used because sample sizes for both stocks were largest there. A multiway frequency table seemed to be the appropriate statistical tool, since counts of grouping codes was the response variable during each set stage and for each stock. However, one of the most important assumptions of multiway frequency analysis, independence, was not met. Only designs for comparisons between subjects may be analyzed with this analysis, so that the frequency in each cell is independent of the frequencies in all other cells. If the same case contributes values to more than one cell, those cells are not independent (Tabachnik and Fidell, 1996). In our study, each case (i.e. each set) contributed to three different cells (the three set stages).

Consequently, to test for differences in dispersion behavior between the stocks, data were rearranged by using the grouping code as the response variable and set stages as the repeated measures in each set (Table 1). Therefore, this design resembled a repeated-measures analysis with one among-subjects factor (stocks) and one within-subjects factor (set stage). If the response variable were in interval scale, a repeated-measures analysis of variance (ANOVA) would have been appropriate to test for differences between stocks (Zar, 1999). However, the response variable in our study was the grouping code, a categorical variable in ordinal scale.

The plausible alternative to apply was logistic regression, often referred to as linear probability models (Tabach-

nik and Fidell, 1996). This technique is similar to multiple regression analysis in that one or more independent variables (the three set stages in our study) are used to predict a single dependent, categorical variable (the stocks). Linear probability models accommodate all types of independent variables (numerical and categorical) and they do not have to be normally distributed, linearly related, or of equal variance within each group. The assumptions of multivariate normality and equal variance-covariance matrices across groups do not have to be met, either. Furthermore, logistic regression might be preferable to multiple discriminant analysis because it is similar to regression with its straightforward statistical tests, ability to incorporate nonlinear effects, and wide range of diagnostics (Tabachnik and Fidell, 1996).

The model produced by logistic regression is nonlinear, and the outcome variable is the probability of having one outcome or another (in our study: one stock or the other) based on a nonlinear function of the best linear combination of predictors, with two outcomes (Tabachnik and Fidell, 1996):

$$\hat{Y}_i = \frac{e^u}{1+e^u},$$

where $\hat{Y}_i$ = the estimated probability that the ith case is in one of the categories and u is the usual linear regression equation:

$$u = A + B_1X_1 + B_2X_2 + \ldots + B_kX_k,$$

with constant A, coefficients B_j, and predictors, X_j (independent variables, the set stages in this study) for k predictors (j=1, 2, ..., k).

This linear regression equation creates the log of the odds, that is, the linear regression equation is the (natural log of the) probability of being in one group divided by the probability of being in the other group. The procedure for estimating coefficients is maximum likelihood, and the goal is to find the best linear combination of predictors to maximize the likelihood of obtaining the observed outcome frequencies. Logistic regression can be used to fit and compare models. The researcher uses goodness-of-fit tests to choose the model that does the best job of predictions with the fewest predictors. (Tabachnik and Fidell, 1996).

Therefore, logistic regression analysis was applied to test the predictability of stock membership (the dependent or grouping variable) by grouping codes (response variables) during three set stages (independent variables). The simplest model (constant-only model) was compared with the full model (with the three independent variables) by computing their log-likelihoods and by using χ^2. Degrees of freedom were the difference between degrees of freedom for the full and the constant-only models. The constant-only model has 1 df (for the constant) and the full model for our study had 3 df (1 df for each individual effect and one for the constant); therefore χ^2 was evaluated with 3 df. If χ^2 was significant, the full model would be reliable (Tabachnik and Fidell, 1996).

Results

Spatial patterns in evasive behavior of northeastern offshore spotted dolphins

The evasion index by set of northeastern offshore spotted dolphins was averaged in 2 × 2 quadrants and the resulting contour map is shown in Figure 1. The highest evasion index by set contour was 60% and extended approximately from south of the Baja California peninsula, across the Gulf of California mouth, and to the Mexican mainland (approx. 20 northern latitude). The 55% and 50% evasion

Table 1

Repeated-measures design to test for differences in dispersion behavior[1] between northeastern offshore spotted and eastern spinner dolphins. The data (response variable) are grouping codes for case i, during set stage j, for species k (=X_{ijk}). (Mexican fleet, 1992–95, PNAAPD data.)

			Set stages		
Case (herd in each set)		Species	1 (before chase)	2 (during chase)	3 (during encirclement)
1 to 308	1	northeastern offshore spotted dolphin	$X_{1\,1\,1}$	$X_{1\,2\,1}$	$X_{1\,3\,1}$
			$X_{308\,1\,1}$	$X_{308\,2\,1}$	$X_{308\,3\,1}$
309 to 544	2	eastern spinner dolphin	$X_{309\,1\,2}$	$X_{309\,2\,2}$	$X_{309\,3\,2}$
			$X_{544\,1\,2}$	$X_{544\,2\,2}$	$X_{544\,3\,2}$

[1] Herd dispersion: to establish if a herd dispersed during a set, the grouping codes applied by the observers in paragraph 3 of the RMMOSD were used. The codes are the following: 1, herd is in one group; 2, herd has divided into two or three groups; 3, herd consists of more than three groups. These codes were recorded during the three set stages: before chase, during chase, and during encirclement. If observers documented an ascending order in the codes (1, 2, 3), this feature was interpreted as herd dispersion during the fishing operation.

index contours were approximately parallel to the 60% contour and in addition formed a triangle-shaped area off the coast of Guatemala. Evasion indices 40% and lower extended south and offshore west of Mexico (Fig. 1). Therefore, the 60%, 50%, and 40% contours were considered the limits between three areas with different evasive behavior of the northeastern offshore spotted dolphin for our study. Three areas were identified (shaded areas in Fig. 1):

1) Low evasion: south of Mexico (30% to 40% estimated evasion index by set)
2) Medium evasion: coastal area south of Guatemala (50% to 55% estimated evasion index by set)
3) High evasion: mouth of the Gulf of California (60% and higher estimated evasion index by set)

Not all data between these contours were used because of difficulty in extracting data throughout the geographic range and because sample sizes for each area (n>100) seemed to be adequate for the analysis. Average mean evasion indices differed significantly between the three areas (Kruskal-Wallis, n_1=206, n_2=111, n_3=491; total n=808, H=93.13, 2 df, P<0.0001). Hence, nonparametric multiple comparisons between all pairs of areas were executed, and all pairs were found to be significantly different (Table 2).

According to these results, there seemed to be a spatial pattern in evasive behavior (measured in our study as the estimated median evasion index by set in each evasion area) of northeastern offshore spotted dolphins during fishing operations of the Mexican fleet from 1992 to 1995.

Differences between stocks

The eastern spinner dolphin seemed to evade capture more effectively than the northeastern offshore spotted dolphin in evasion area 3 when estimated evasion indices by set for both stocks were compared (Fig. 2). The differences were significant according to the Kolmogorov-Smirnov one-sided test for two independent samples (spinner: n=275, spotted: n=489; D=0.2031, P<0.001).

With respect to the evasive strategies of these two stocks, evasion index when the dolphins escaped under the net was compared by set. Eastern spinner dolphins apparently escaped more effectively under the net than northeastern offshore spotted dolphins (spinner n=177, spotted n=125, D=0.4097, P<0.001, Kolmogorov-Smirnov two-sample test; Fig. 3).

Dispersion behavior of northeastern offshore spotted and eastern spinner dolphins is presented for evasion area 3 (mouth of the Gulf of California, Fig. 4). Herds of both stocks tended to disperse from one set stage to the next; during encirclement, grouping code 3 (herd divided into more than 3 subgroups) had increased and was the most frequently recorded grouping code for northeastern offshore spotted dolphins in area 3 during our study. Northeastern offshore spotted herds tended to be more fragmented than eastern spinner herds before chase and to disperse in greater numbers during subsequent set stages (Fig. 4). Logistic regression analysis revealed a reliable full model (χ^2=60.209, P<0.001, df 3, n=544), i.e. the outcome of stock was predicted by the three independent variables (set stages). The prediction of stock outcome might further be interpreted as a difference between northeastern offshore spotted and eastern spinner dolphins with respect to dispersion behavior in our study.

In contrast, both stocks presumably escaped only on rare occasions by leaping out of the net because eastern spinners did so in only 5 of 275 sets (1.82%) and northeastern offshore spotted dolphins in 3 of 489 sets (0.61%) during the study period. Estimated evasion indices by set could not be compared because the samples were too small for any statistical test.

Discussion

Spatial patterns in evasive behavior

An apparent significant geographic difference in evasive behavior of northeastern offshore spotted dolphins was found between three areas in the EPO (Mexican fleet data, 1992–95, Fig. 1, Table 2). The lowest evasion area was located south of Mexico (area 1), the medium evasion area was in a relatively small coastal area south of Guatemala (area 2), and the highest evasion area was in the Gulf of California mouth (area 3, Fig. 1). About twenty years ago, fishermen noticed that dolphins were more difficult to capture in some areas than in others. Certain coastal dolphin

Table 2

Nonparametric multiple comparisons (according to Conover, 1980; Neave and Worthington, 1988) of estimated average (median) evasion index by geographic area (see Fig. 2) for the northeastern offshore spotted dolphin (1992–95, Mexican fleet, PNAAPD data). The null hypothesis (i.e. the median of two groups is equal) is rejected if the T statistic is larger than the critical Z value. All pairwise comparisons were significant (*indicates significant at P<0.05, where the critical Z-value for 3 groups (k–1)=2.39).

Area	n	Estimated median evasion index (%)	25–75% quartiles	Pairwise comparisons	T
1 (low)	206	25.00	0–66.67	1 and 2	3.17*
2 (medium)	111	44.44	20–83.33	1 and 3	9.49*
3 (high)	491	71.80	40–92.50	2 and 3	3.86*

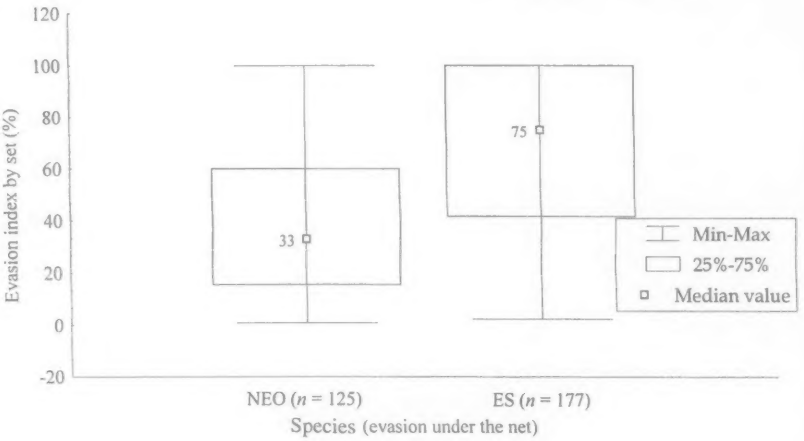

Figure 3

"Box and whiskers" plot for estimated evasion index by set for northeastern offshore spotted (NEO) and eastern spinner (ES) dolphins when dolphins evaded under the net (Mexican fleet, PNAAPD data 1992–95).

herds were called "the untouchables" by fishermen (Pryor and Norris, 1978) because the animals were capable (and still are) of completely evading the fishing operation even before the net has been set (National Research Council, 1992).

Several authors have suggested that the reasons for the detectable spatial patterns in evasive behavior seem to be related to the learning capacity of these mammals. Stuntz and Perrin[5] stated that dolphins (*Stenella* spp.) were more difficult to capture in areas where fishing effort had been greatest, therefore concluding that dolphins have learned to evade capture more effectively. Hewitt (1985) pointed out that the dolphins' reaction distance to survey vessels "may vary between geographic areas with the degree of animal naivete." This possibility was also considered by Hall and Boyer (1986) as an explanation for the spatial heterogeneity of mortality rates.

Although dolphin learning seems to be a logical explanation for geographic differences in evasive behavior, adequate measures for the dolphins' experience (i.e. their exposure to the tuna fishery) have to be designed. A measure may be the historical fishing effort (no. of chases per one-, two- or five-degree quadrant by the international fleet on the northeastern offshore spotted dolphin accumulated from 1959, when the tuna purse-seining fishery started, until today) standardized with respect to herd density (as described by Polachek, 1987; Reilly, 1990; or Reilly and Fiedler, 1994). Standardization is necessary because dolphins in areas with fewer herds will presumably have more opportunities to practice evading capture in comparison with areas where there are more herds (higher density) and effort has apparently been the same (number of chases per quadrant).

Furthermore, the number of dolphins that evaded capture during a set might also be affected (reduced) by the number of speedboats, the fishing vessel's power, and the presence of a helicopter; explosives were also used to herd dolphins several years ago. In addition, the dolphins' distribution (and hence possibly the fleet's effort) is influenced by changes in oceanographic features between seasons (Au and Perryman, 1985; Reilly, 1990) and years (Fiedler and Reilly, 1994; Reilly and Fiedler, 1994). Therefore, all variables recorded by the observers regarding the fishing operation (vessel power, number of speedboats, aerial assistance, use of explosives), time, and environmental features should be considered. However, this thorough analysis, including the important (according to the literature) variable "fishing effort" was not performed with the available data because the effort of the Mexican fleet should not be considered representative of the international fleet (Mexican vessels tend to fish closer to Mexico than do other fleets). Our future research aims to consider these variables and the effort of the complete international fleet, which is possible only with data from the IATTC.

Differences between stocks

In the mouth of the Gulf of California (area 3, Fig. 1), eastern spinner dolphins (*Stenella longirostris orientalis*) showed significantly higher estimated evasion indices than those for northeastern offshore spotted dolphins (*Stenella attenuata*) in our study (Fig. 2). A stronger evasion behavior by the eastern spinner dolphin has been described by other authors (Norris et al., 1978; Pryor and Kang, 1980) and may relate to different evasive strategies used by the two stocks to evade capture in the net, some of which were analyzed in our study.

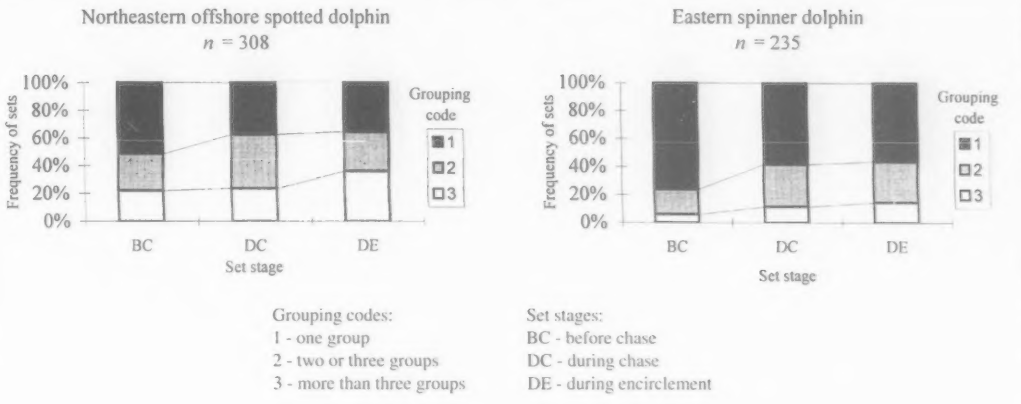

Figure 4

Dispersion (the ability of herds to "explode" (separate suddenly) into subgroups in relation to their configuration before chase) of northeastern offshore spotted and eastern spinner herds in evasion area 3 (Gulf of California mouth, Mexican fleet, PNAAPD data 1992–95).

Analysis of evasive strategies indicated that eastern spinner dolphins seemed to evade capture more effectively under the net than northeastern offshore spotted dolphins (Fig. 3). According to stomach-content analyses of spinner and spotted dolphins, the spinner dolphin is thought to forage deeper (approx. 250 m) than the spotted dolphin (approx. 30 m) (Fitch and Brownell, 1968). Therefore, the spinner dolphin may be more habituated to dive deeply enough to escape under the bottom of the net approximately 200 m from the surface, before the net is pursed.

In addition, even though herds of both stocks tended to disperse from one set stage to the next, there seemed to be a significant difference in dispersion between the stocks (according to logistic regression analysis results), i.e. eastern spinner dolphins apparently dispersed less often than the northeastern offshore spotted (Fig. 4). This evasive strategy (previously described as "school exploding" by Allen et al., 1980) also might have contributed to the eastern spinner dolphin's higher estimated evasion index in our study (Fig. 2). Because they disperse less and also tend to form larger subgroups than spotted dolphins during the fishing operation (Pryor and Kang, 1980), eastern spinner dolphin herds could be more cohesive and this behavior may coordinate their evasive movements more effectively than northeastern offshore spotted dolphins.

Moreover, the apparent higher evasive ability of eastern spinner dolphins might also be associated with different activity levels in these dolphins. Spinner dolphin activity level during the set tends to be higher than that of the spotted dolphin (Schramm, 1997) and could probably enhance evasion by spinners.

The frequency of evasion over the net was negligible in both stocks (spotted dolphins leaped over the net in only 0.61% of the sets analyzed; spinners, in 1.8%). Fishermen and scientists (Pryor and Kang, 1980) have also observed that dolphins encountered in fishing for tuna seldom attempt to leap out of the net to escape, even though individuals of both dolphin species are capable of doing so. The reasons why this event seems to be so rare are still unknown. Norris et al. (1978) mentioned that oceanic dolphins (like spinners and spotted) in captivity may take more time than coastal dolphins (like bottlenose dolphins, *Tursiops truncatus*) to cross a white line or a sunken rope on the tank bottom; this behavior might be explained by the fact that the animals may come from open waters where no barriers are present at all and there is no confinement. Thus, confinement in a tuna set may be foreign to these animals, as are the corkline and other features of a set (Norris et al., 1978).

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Larval growth of the anchoveta *Engraulis ringens* during the winter spawning season off central Chile

Eduardo H. Hernandez

Leonardo R. Castro*

Departamento de Oceanografia
Universidad de Concepcion
Casilla 160-C, Concepcion. Chile

E-mail address (for L. R. Castro, contact author): lecastro@udec.cl

Abstract–Larval growth rates of the anchoveta *Engraulis ringens* were determined for two periods during the winter spawning season off Talcahuano, central Chile. Because winter is the season of minimum plankton production during the year, we hypothesized that larval growth rates during winter should be constantly low because of decreased larval fish food availability. Our results, however, indicate that 1) mean larval growth rates determined from three growth models in winter (mid-July through mid-September) were as high as in other periods of the year (linear, Gompertz, and von Bertalanffy; 0.47 mm/d, 0.50 mm/d, and 0.48 mm/d, repectively); 2) differences in larval growth rates occurred in two groups of cohorts spawned in the two periods during the spawning season (0.40 mm/d vs. 0.57 mm/d); and, 3) larval food (dinoflagellates, copepod eggs, and copepod nauplii) concentrations in the field were relatively high and not very variable during the study. Hydrography of the water column, however, varied throughout the season. During the last weeks of the study seawater temperature was higher, indicating intrusion of offshore warmer waters into the coastal zone. The presence of these warmer waters suggests that differences in growth rates between groups of cohorts may have resulted from larval development in water with different characteristics. Consequently, for a coastal upwelling species such as the anchoveta, increased growth rates in some cohorts may be advantageous considering that its main spawning season occurs in winter when the environmental conditions fluctuate markedly in short time scales.

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The anchoveta *Engraulis ringens* (also known as "Peruvian anchoveta," FAO, 1988) has traditionally been one of the most important pelagic resources in the world in terms of landings (Pauly and Palomares, 1989). After strong fluctuations in abundance during the last three decades, especially marked during the anchoveta collapse in the early seventies, the stocks have rebounded. Catches in recent years have reached over 12 million tons and constitute one of the largest fisheries of the world.

Within its long latitudinal distribution range from 4°S to 40°S, several major spawning areas have been reported. The most important spawning areas have been traditionally located off Northern Peru, from off Southern Peru to off Northern Chile, and off Central Chile (Bernal et al., 1983). Despite its wide latitudinal range and paramount economic importance for the world fish markets, other than distribution and abundance, little information exists on basic biological parameters during the larval phase. For the larval stage, reseachers have documented information on the age of onset of feeding, feeding habits, and validation of daily deposition of ring increments in the otoliths (Rojas de Mendiola and Gómez, 1980, 1981; Ware et al., 1981; Muck et al., 1989; Morales-Nin, 1989; Villavicencio, 1989; Llanos, 1990). Information on larval growth rates in the wild, however, have been reported only for the southern stock and, unfortunately, only for seasons other than the major winter spawning seasons (Herrera et al., 1985).

There is a marked seasonality in the southern spawning area of the anchoveta. During spring, summer, and early fall, southerly winds predominate and lead to very intense upwelling events. During winter, intense northerly winds dominate, and upwelling events develop only occasionally. This marked seasonality in the oceanography also leads to changes in environmental conditions that may affect larval growth. During winter, due to the low frequency of upwelling events, the general production of the area is lower than in summer. Similarly, the very intense north winds may produce high levels of turbulence in the water column, thus dispersing the potential larval food patches (Lasker 1975, 1978). On the basis of these harsh environmental conditions, it has been proposed that food for larval anchoveta off Talcahuano might be limited during winter (Herrera et al., 1985; Bernal et al., 1990). However, because the anchoveta has been historically an important fishery of central Chile (1996 landings in the area reached ca. 300,000 metric tons, SERNAPESCA, 1996), there must be some mechanisms by which relatively high levels of larval survival can be achieved: either feeding conditions are not permanently harsh or factors other than food enhance larval survival, at least for some periods within the winter spawning season.

The objectives of our study were 1) to determine whether intraseasonal differences in growth rates occur between groups of cohorts of larval anchoveta spawned throughout the winter spawning season, and 2) to assess the role of two environmental factors (larval food and temperature) as potential factors affecting larval growth rates. Because some basic information for the deter-

mination of growth rates was still missing, we first determined the age of deposition of the first ring increment on larval otoliths and then described the growth functions of larvae caught in the wild, using three common growth models (the linear, Gompertz, and von Bertalanffy). Finally, we determined the mean growth rates for larval anchoveta spawned over the entire sampling winter season, and for two groups of cohorts spawned during that season but which faced different environmental conditions.

Methods

Larval growth in the wild

Larval anchoveta were collected in eight cruises from a grid of nine stations in the coastal zone off Talcahuano, central Chile (Fig. 1), during the winter of 1995 (12, 18 July; 1, 8, 17, 30 August; 4, 11 September). In each cruise, ichthyoplankton samples were collected with a bongo net (mesh size: 500 µm, diameter of mouth of net: 60-cm) equipped with a flow meter to quantify the volume of water sampled from the surface to a depth of 40 m. Once on board, half of the samples were preserved in 4% formalin and the other half in 96% ethanol for otolith analysis. At all stations, sea water samples were collected from nine depths (0, 5, 10, 15, 20, 30, 40, 60, 80 m) in 4-liter Niskin bottles for determination of temperature and salinity, and for identification and quantification of microplankton (dinoflagellates, copepod eggs, and copepod larvae) as potential larval food.

In the laboratory, anchovy larvae from both subsamples were identified, sorted, and counted. From the subsamples preserved in ethanol, 112 larvae within a size range between 5.68 and 20.74 mm (corrected for shrinkage, see below) were measured and their otolits were extracted and mounted in immersion oil. Otolith ring counts and otolith diameters were determined with the aid of a light microscope attached to a video camera and monitor to facilitate the reading of daily rings. Each otolith was counted twice and those counts where the readings differed in three or more rings were discarded. Larval lengths were corrected for shrinkage by using the algorithms proposed by Theilacker (1980) for larval northern anchovy (*Engraulis mordax*). Three models were used to describe the growth and growth rates of larval anchovy: the linear, Gompertz, and von Bertalanffy models. These models were used to describe growth for 1) all larvae spawned during winter (1 July–11 September) of 1995, and 2) for two groups of cohorts spawned during a) 1 July through 17 August, and b) from 18 August through 11 September. To classify the larvae as belonging to the first or second period, spawning dates were backcalculated as "the number of rings + 2" (see day of first ring deposition in the "Results" section). All statistical tests (regressions, analyses of variance, covariance, and models) were carried out with the commercial statistical software package STATISTICA, 1993.

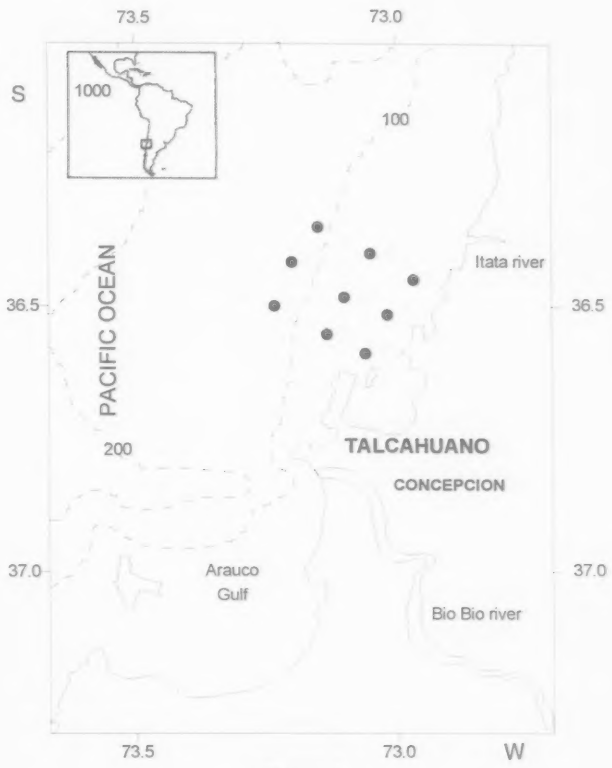

Figure 1

Survey area of ichthyoplankton during the 1995 anchoveta winter spawning season off Central Chile. Dots represent sampling stations.

First increment deposition

Anchovy eggs were collected from a coastal station off Talcahuano during the winter spawning season on 1997. At that station, gentle vertical tows were carried out with a bongo net from 0 to 40 m for collections of ichthyoplankton. The samples were placed in a 20-gal cooler at 12–13°C and transported to the Universidad de Concepcion Marine Station at Dichato. The transit time to the station took about 45 min. At the laboratory, between 20 and 60 anchovy eggs were sorted and placed in ten, 700-mL transparent plastic jars and incubated at 10°C and 14°C in light and dark cycles of 14:10 h and 12:12 h, respectively. One third of the water contained in the jars was replaced daily throughout the duration of the study. All larvae hatched in a given day were transplanted to new jars containing water at the same temperature as that used for hatching and in which *Isocrysis* sp. and powdered larval food were added daily. Every day a variable number of larvae were extracted from the jars for determination of fresh larval length, preserved in ethanol, remeasured, and dissected for otolith analysis (ring counts and diameter).

Results

First increment deposition

Only thirteen larvae from the rearing experiments in the laboratory were analyzed for determination of age at the first increment deposition, and because of the low number of larvae, the data from the treatments were analyzed together. These preliminary experiments showed that no larvae formed the first ring on the otoliths at hatching (two larvae were analyzed at hatching). Although the first ring on the otoliths was first observed in a larva at end of the first larval day after hatching (two larvae were analyzed), most larvae formed their first ring during the third day after hatching (four out of six larvae, 3-days-old or older). The larva analyzed at the end of the fourth day had two rings deposited; therefore it formed its first ring during the third day. At the end of the third day after hatching, all larvae had deposited their first ring. The mean diameter of the otolith focus for those larvae hatched in our experiments was 10.23 (SD=1.25) µm and the mean diameter of the otolith with their first increment formed was 12.83 (SD=1.56) µm.

The relation between the number of rings and otolith diameters from anchoveta larvae collected in the wild was well described by a linear regression (r^2=0.90; n=112; P<0.001)(Fig. 2). From this relationship, a larval anchoveta with one ring should have an estimated otolith diameter of 12.6 micrometers, which is close to the mean otolith diameter measured from larvae reared in our laboratory (mean=12.83 µm, SD=1.56). A power model was used to describe the relation between otolith diameter and larval length (corrected for shrinkage after Theilacker 1980) of wild larvae (r^2=0.79; n=112; P<0.001) (Fig. 3). According to these two relationships, a larva with one increment (12.6-µm otolith diameter) should have a larval length of 5.6 mm.

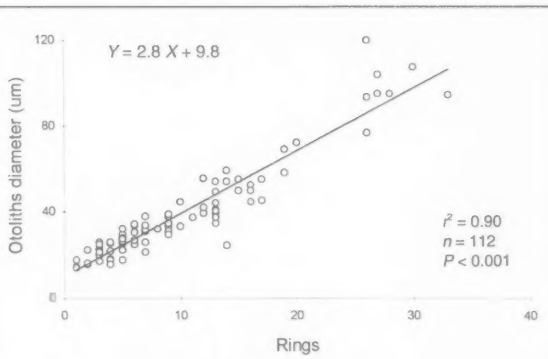

Figure 2

Linear regression showing the relation between the number of otolith rings formed and the otolith diameters of anchoveta larvae caught in the wild.

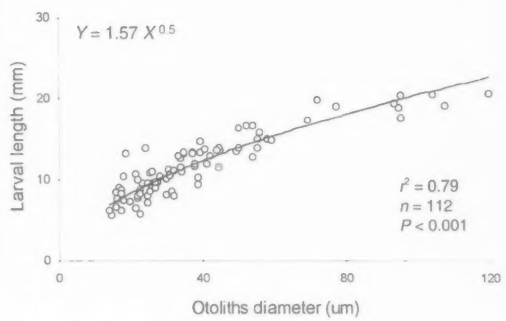

Figure 3

Relation between otolith diameter and length in larval anchoveta during the winter spawning season of 1995.

Larval growth of larvae caught in the wild

Because deposition of the first ring in most larvae occurred during the third day after hatching, age of larvae caught in the wild was estimated by adding two days to the number of rings in their otoliths. The standard lengths of larvae used in the growth models varied between 5.68 mm and 20.74 mm, and their age ranged from 3 to 35 days.

The three growth models used to describe anchovy larval growth during the winter of 1995 were highly significant (P<0.001) (Fig. 4, Table 1). The linear model yielded a daily growth rate of 0.47 mm/d (n=112 larvae; r^2=0.82); the Gompertz model yielded a mean daily growth rate of 0.50 mm/d (n=112 larvae; r^2=0.84); and the von Bertalanffy model yielded a mean daily growth rate of 0.48 mm/d (n=112 larvae; r^2=0.84). Estimated larval length at the end of the third day after hatching (day of the first ring deposition) varied from 7.81 mm with the linear model to 7.17 mm with the Gompertz model and 6.13 mm with the von Bertalanffy model.

The results of the analyses of growth rates between groups of cohorts spawned early versus late in the winter season varied according to the models used to describe growth. The larval growth rates determined from the linear model revealed that the group of daily cohorts spawned earlier in the season grew slower (1 Jul–17 Aug: 0.40 mm/d; n=63) than the group of larvae spawned later in the season (18 Aug–11 Sep: 0.57 mm/d; n=49) (ANCOVA, F=26.2, n=112, P<0.001; Zar, 1984). For both groups of cohorts, the linear regressions used to describe larval growth were significant (P<0.001) and explained over 78% and 74% of the variance in the respective data sets. A comparison of larval growth rates between periods using the Gompertz and von Bertalanffy models, however, showed no differences between larvae spawned early versus larvae spawned later in winter (Gompertz: F=1.08, n=112, P>0.05; von Bertalanffy: F=0.82, n=112, P>0.05; analysis of residual sum of squares, ARSS; Chen et al., 1992).

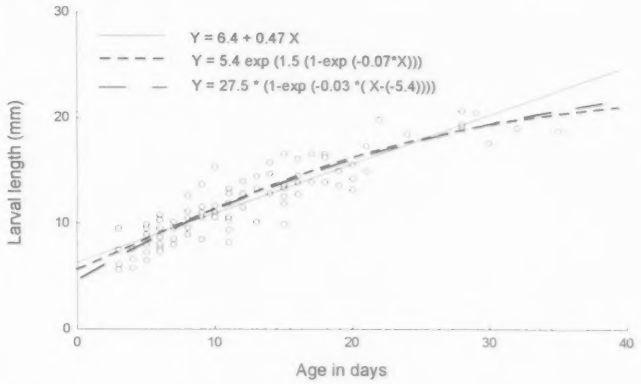

Figure 4

Models usedd to describe larval growth of the anchoveta *Engraulis ringens* during the 1995 winter spawning season off central Chile: linear model (—); Gompertz model (– – –); and von Bertalanffy model (— — —). Basic statistics for each model are shown in Table 1.

Table 1

Growth models used to determine growth rates for larval anchoveta off central Chile during the 1995 winter spawning season (mid July through mid September). RSS = residual sum of squares; r^2 = coefficient of determination.

	Model	Parameters	RSS	r^2	P
Linear	$Y = a + bX$	$a = 6.4$ $b = 0.47$	254.1	0.82	<0.001
Gompertz	$L = L_0 \exp(G(1 - \exp(-gt)))$	$L_0 = 5.4$ $G = 1.5$ $g = 0.07$	227.7	0.84	<0.001
von Bertalanffy	$L = L_\infty(1 - \exp(-K(t-t_0)))$	$L_\infty = 27.5$ $K = 0.03$ $t_0 = -5.4$	227.1	0.84	<0.001

Larval food (dinoflagellates, copepod eggs, and nauplii) occurred in relatively high concentrations throughout the season (Fig. 5). No differences in dinoflagellate densities (Mann-Whitney U=4.00; P=0.296), copepod egg densities (Mann-Whitney U=7.00; P=0.861), and copepod nauplii densities (Mann-Whitney U=5.00; P=0.456), were detected between the periods used to classify both groups of larval cohorts during the season. Sea surface temperature, another factor that may affect larval growth, was higher (Mann-Whitney U=19; P=0.025) during the second period of the spawning season (maximum. sea surface temperature: 13.5°C), probably as a result of the intrusion of offshore warmer waters to the coastal zone (Fig. 6) During the first period of the season, instead, when some of the upwelling events and the river plume were stronger and farther offshore (Castro et al., 2000), the sea surface temperature reached a minimum (11.1°C) in the coastal area.

Discussion

The deposition of the first ring in the larval otoliths has been associated with events in the early life history of fishes, such as the onset of feeding or eye pigmentation. For northern anchovy, *Engraulis mordax*, for instance, the deposition of the first increment takes place at the initiation of exogenous larval feeding or after yolksac absorption which occurs five or six days after hatching (Brothers et al., 1976; Methot and Kramer, 1979). Bay anchovy, *Anchoa mitchilli*, completes its first otolith ring

at the end of the second day after hatching—a time which corresponds to the time of yolksac depletion (Leak and Houde, 1987). Mediterranean anchovy, *Engraulis encrasicolus*, deposits its first increment during the second day after hatching with completion of yolk absorption (Palomera et al., 1988). In our rearing experiments larval anchoveta finished forming their first otolith increment at the end of the third day after hatching, which coincides with the end of the eye pigmentation.

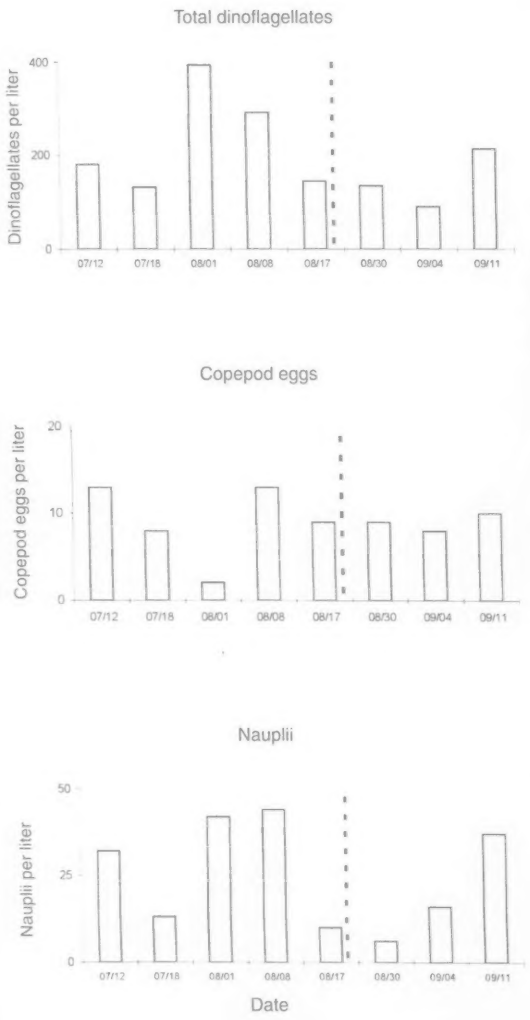

Figure 5

Mean density of potential larval food items in field during the winter spawning season of the anchoveta *Engraulis ringens* off Talcahuano, central Chile, in 1995: dinoflagellates, copepod eggs, and copepod nauplii. The vertical dashed line indicates the separation of periods considered in the groups of larval cohorts.

Larval anchoveta finished forming their first otolith increment at a larval length of 5.6 mm (estimated from the rings and otolith diameter and from the otolith diameter and larval length relationships). Observations of laboratory-reared anchoveta (*E. ringens)* larvae off Peru indicated that the mouth and eyes become functional at 64 h after hatching at a larval length of 4.03 mm (Ware et al., 1981). Initiation of larval feeding, however, varied from 3.5 to 6.8 days after hatching (mean 4.4 d), which corresponded to estimated larval lengths between 4.10 and 4.16 mm. If the deposition of the first ring in larval anchoveta coincided with the onset of feeding, then our estimations of 5.6 mm at the end of the third day after hatching were slightly higher than those estimated by Ware et al., (1981).

The three models used to fit the age and larval length data of anchoveta larvae collected during the winter spawning season in 1995 fitted the age and larval anchovy length data appropriately for the winter spawning season of 1995. A visual inspection, however, revealed a slight decrease in growth rate as the larvae increased in age, which suggests that the nonlinear models (von Bertalanffy and Gompertz) would describe larval growth better beyond the ages determined in our study.

Growth rates calculated with the three growth models (linear=0.47 mm/d; Gompertz=0.50 mm/d; and von Bertalanffy=0.48 mm/d) were very similar to estimations for anchoveta in other seasons (larval size range 5.0–20mm=0.45 mm/d, 12.5°C, Herrera et al., 1985) and within ranges reported for other engraulids. Methot and Kramer (1979) estimated northern anchovy larval growth rates between 0.34 and 0.55 mm/d between 13.0° and 16.2°C; for bay anchovy, *Anchoa mitchilli*, larval growth rates between 22° and 30°C ranged from 0.25 to 0.58 mm/d (Fives et al., 1986; Leak and Houde, 1987; Castro and Cowen, 1991); and for Mediterranean anchovy, *Engraulis encrasicolus,* growth rates ranged between 0.9 and 0.96 mm/d for 8-mm larvae at 20°C (Palomera et al., 1988). If only the larval anchovies from the upwelling areas of California and central Chile are compared, then the growth rates determined for the anchoveta in our study (0.40–0.57 mm/d at sea temperatures between 11.1° and 13.5°C), are slightly higher than those estimated for the northern anchovy at similar temperatures (0.39–0.47 mm/d at 13.0–13.2°C; Methot and Kramer 1979).

Some intraseasonal variability in growth rates of the anchoveta was observed between groups of cohorts during the winter spawning season, when rates from linear growth models were compared. Larval growth rates determined with the linear model (0.40 vs. 0. 57 mm/d) were within the same range reported for cohorts of other clupeiforms spawning at different times during the year or under different environmental conditions within the same spawning season (Methot and Kramer, 1979, Leak and Houde, 1987). Larval food, as a potential factor affecting larval growth rates, did not seem to be limited throughout the

entire sampling season. In fact, observed larval food concentrations may be considered high compared with concentrations reported for the same species in lower latitudes (Walsh et al., 1980). Differences in seawater temperature experienced by both groups of cohorts spawned during winter, however, may have accounted for the apparent differences in larval growth rates. An increase in water temperature occurred during the last weeks of sampling owing to an intrusion of offshore warmer waters into the coastal zone (Castro et al., 2000). Response to changes in seawater temperature as the spawning seasons progress is known for other anchovy species (*A. mitchilli*, Leak and Hode, 1987; Rilling and Houde, 1999). However, earlier evidence may have not been so conclusive for larval anchovy at upwelling areas (i.e. *E. mordax*, Methot and Kramer, 1979; Butler, 1989), probably because of the difficulties of determining the temperature of the water where the larvae actually developed, especially given the frequent changes in hydrographic conditions common in coastal upwelling areas.

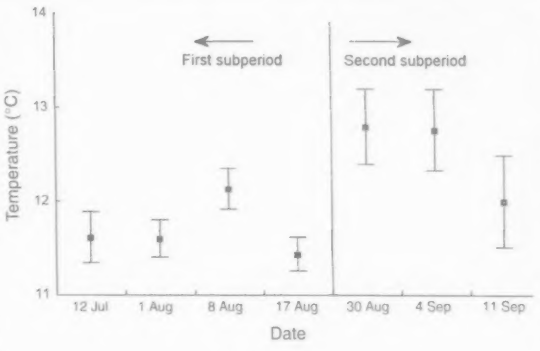

Figure 6

Mean sea surface temperature during the winter spawning season of the anchoveta *Engraulis ringens* off Talcahuano, central Chile, in 1995.

Because growth may be dependent on environmental factors (Pepin, 1991), seasonal variations in growth rates were expected among the cohorts spawned during the year. In our study, we documented potential differences in growth rates of groups of cohorts spawned a few weeks apart during the main spawning season. For coastal species living in upwelling areas, changes in growth rates among cohorts may be beneficial because environmental conditions may change markedly in short time scales (from days to a few weeks). With this scenario, increases in growth rates in some cohorts (given the right conditions during a few weeks) may be advantageous because the main spawning season for *E. ringens* occurs in winter. At the end of the season we expected a large pool of late larvae and early juveniles within a similar size range that had grown at different rates because they were exposed to different conditions. Given the relationship between environmental conditions and larval development, and the wide distribution range of the anchoveta (from 4°S to 40°S), differences in growth rates are to be expected in larval anchovies growing in different latitudes. Future studies should evaluate whether the models and growth rate changes determined off Talcahuano (37°S), close to the southern limit of distribution for the anchoveta, also apply for larvae growing in lower latitudes, such as spawning areas off northern Chile (18–24°S) and Peru (4–14°S).

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Biology and ecology of threaded sculpin, *Gymnocanthus pistilliger*, in the eastern Bering Sea

Gerald R. Hoff
National Marine Fisheries Service
Alaska Fisheries Science Center
7600 Sand Point Way NE
Seattle, Washington 98115
E-mail address: jerry.hoff@noaa.gov

Abstract–The threaded sculpin (*Gymnocanthus pistilliger*) is distributed in the North Pacific from Norton Sound south to Southeast Alaska and west to Russia and Japan. It reaches its greatest abundance in the eastern Bering Sea in Bristol Bay where it is typically found in waters less than 50 m deep. Alaska Fisheries Science Center groundfish surveys in the eastern Bering Sea have estimated densities of up to 102 fish per hectare (catch per unit of effort, CPUE) for 1997 and 1998. Population estimates for 1997 were 111.20 million and for 1998 were 51.70 million. The population estimate drop is reflected in length-frequency data that suggest a complete lack of 2-year-old fish for 1998. *Gymnocanthus pistilliger* is a short-lived species (age estimates from otoliths range up to 10 years for males and up to 9 years for females), and the maximum size is 161 mm and 201 mm total length for males and females, respectively. During June, when specimen collections were made, ovaries are in the resting stage and contain some residual eggs from a previous spawning. The diet of *G. pistilliger* changes from predominantly gammarid amphipods and polychaetes to crangonid shrimp and fish with increased total length. Comparisons with studies from the western North Pacific on *G. pistilliger* suggest biological differences between populations, which may reflect adaptation to different habitats.

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Gymnocanthus pistilliger (Pallas), the threaded sculpin, is a small marine cottid that inhabits waters from Southeast Alaska north to Norton Sound and west to Russia and Japan (Wilson, 1973). It is found in shallow waters (<50 m) over soft sandy to muddy bottoms and is the most abundant cottid in the Bristol Bay region (>15 m) of the eastern Bering Sea. *Gymnocanthus pistilliger* may compete for resources with juvenile stages of commercially important flatfish in the shallow bays and nearshore areas used as nursery grounds (Grigorev and Fadeev, 1995). Although *G. pistilliger* is an abundant species, little life history information is available on Bristol Bay populations. The present study reports on the ecology and biology of *G. pistilliger* from Bristol Bay, Alaska, and compares it to ecology studies conducted on western North Pacific populations.

Methods

Specimens of *G. pistilliger* were collected in June of 1997 and 1998 during the National Marine Fisheries Service, Alaska Fisheries Science Center (AFSC), eastern Bering Sea survey. The survey area extended from the Alaska Peninsula north to Nunivak and St. Matthew Islands, and west to the 200-m shelf break (Fig. 1). Trawls were conducted on a grid of 356 fixed stations (20 nmi × 20 nmi) fished during daylight hours throughout the Bering Sea survey area. Thirty-minute trawls towed at 3.0 knots were conducted at each station. The shallowest depth surveyed was 15 m in Bristol Bay and the deepest was 178 m near the shelf edge. Trawling was conducted with the AFSC 83-112 eastern trawl, which is a low-opening two-seam trawl with a 26.5-m headrope and 34.1-m cable footrope (Rose and Walters, 1990) wrapped with rubber stripping and chain hangings that contact the bottom while the trawl is towed. Height and width measurements of the net were recorded with an acoustic SCANMAR net mensuration system. Global positioning system was used to record latitude and longitude data at the start and end of the trawl in order to determine distance fished.

The entire catch was sorted to species, enumerated and weighed, or a weighed subsample was used if there was a very large catch. Catch per unit of effort (CPUE) was calculated as number of fish per hectare (no./ha) by dividing the number of fish caught for each haul by the estimate of the area swept (net width × distance fished). *Gymnocanthus pistilliger* occurred in the survey area only at stations less than 50 m in depth (Fig. 1); therefore only this area was used for calculating population estimates. A population estimate was calculated by first determining a mean CPUE from all hauls combined (<50 m) and then expanded to the area. The biomass estimates were calculated in a similar manner by using weight in metric tons. The population and biomass estimates were made under the assumption that all fish in the path of the trawl were caught and were a representative sample for each station grid. However, given that there may be gear selectivity for fish size and given the patchy nature of fish distributions, the populations and biomass stated in this study are best estimates.

In May of 1995 and June of 1988–91 exploratory trawling was conducted in the shallow bays (<30 m) within Bristol

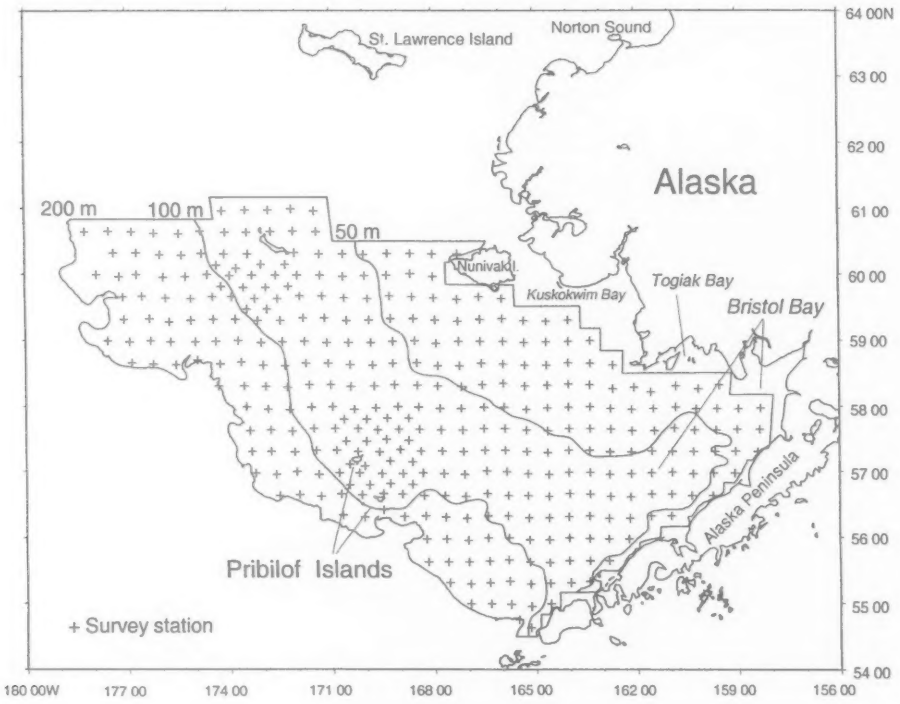

Figure 1

Map of the area in the eastern Bering Sea surveyed by the National Marine Fisheries Service. All stations (+) shown were trawled in 1997 and 1998. Map includes contour lines at 50-, 100-, and 200-m depths.

Bay by the National Marine Fisheries Service. Trawling methods, population, and density estimates were performed as described above.

Gymnocanthus pistilliger samples collected during 1997 and 1998 were preserved at sea by freezing or by preserving in a 10% formalin-seawater solution buffered with sodium bicarbonate. Frozen samples were partially thawed, and total length (TL, in mm), standard length (SL, in mm), total fish weight (TFW, in mg), gonad weight (GW, in mg), and sex were recorded. Sagittal otoliths were removed and placed in 50% ethanol. Parameters from formalin-preserved specimens with stomachs and ovaries removed were recorded in a similar manner and placed in 50% ethanol.

Dark bands on otoliths were evident under reflected light and were counted by the break-and-burn method to ensure inclusion of all ring structures. Length at age was described by using nonlinear regression to fit the von Bertalanffy (1957) growth model for male and females separately with pooled data from the two years.

The von Bertalanffy growth curve is

$$L_t = L_\infty [1-e^{-K(t-t_0)}].$$

Fish numbers for length-frequency samples were combined for all hauls by sex and year.

The relationships of total fish length (TL) to total fish weight (TFW) were investigated with the model

$$TFW\,(\mathrm{g}) = a\,TL(\mathrm{mm})^b.$$

Ovaries were removed and weighed to the nearest milligram from formalin-preserved fish. The gonosomatic index (GSI) was calculated from TFW and ovary weight was calculated as

$$100(ovary\ weight/TFW).$$

Stomach contents were recorded to the lowest practical taxon, and enumerated and weighed to the nearest milligram. For analysis, prey items were grouped into seven logical or taxonomic categories (Table 1). *Gymnocanthus pistilliger* were grouped into four length groups (<100 mm, 100–124 mm, 125–149 mm, and 150–201 mm TL). Percent frequency of occurrence, total count, and total weight were calculated for individual prey items and for each prey item group. Statistical analysis and graphing were conducted with the computer programs Statgraphics 2.0 and SigmaPlot 4.0, and distributional maps were produced with the software Arcview 3.0.

Table 1

Diet composition of *Gymnocanthus pistilliger*. Prey items are grouped into major taxonomic or similar groups and frequency of occurrence (freq.), total count, and total weight percentages were calculated for both individual items and for groups. (Total lengths 73–201 mm, n=93).

Prey items	Frequency of occurrence	Total count	Total weight
Wormlike organisms			
Polychaeta	47.19	1.21	14.27
Echiurus sp.	7.87	0.36	1.43
Opheliidae	2.25	0.03	0.48
Annelida	1.12	0.01	0.01
Goniadae	1.12	0.07	0.08
Total	52.81	1.69	16.26
Amphipoda			
Gammaridea	82.02	92.74	15.43
Caprellidea	2.25	0.04	0.05
Amphipoda unidentified	1.12	0.03	0.26
Total	83.15	92.84	15.74
Shrimp			
Crangonidae	32.58	0.7	31.23
Total	32.58	0.7	31.23
Other Crustacea			
Ostracoda	1.12	0.06	0.01
Mysidacea	1.12	0.01	0.03
Cumacea	17.89	0.4	0.47
Isopoda	1.12	0.01	0.07
Euphausiacea	1.12	0.01	0.02
Crustacea unidentified	1.12	0.01	0.07
Total	21.35	0.52	0.67
Mollusca			
Gastropoda	10.11	0.27	0.64
Naticacea	2.25	0.04	0.99
Bivalvia	31.46	1.39	1.5
Clinocardium sp.	1.12	0.01	1.1
Octopus sp. (beaks)	2.25	0.03	0.01
Total	39.33	1.75	4.24
Fish			
Lumpenus sp.	1.12	0.01	2.24
Ammodytes hexapterus	4.49	0.07	12.03
Teleostei unidentified	2.25	0.03	1.24
Total	7.87	0.12	15.5
Miscellaneous			
Forminifera	3.37	0.07	0.02
Anthozoa	2.25	0.03	0.05
Urochordata	1.12	0.03	0.03
unidentified eggs	10.11	0.48	0.06
organic material unidentified	85.39	1.15	12.28
wood	1.12	0.01	0.19
rocks	38.2	0.51	2.61
sand	4.49	0.06	1.06
material unidentified	1.12	0.01	0.04
Total	88.76	2.37	16.35

Results

Distribution

The distribution of *G. pistilliger* during the 1997 and 1998 eastern Bering Sea surveys was limited to depths <50 m; areas of highest concentration were located around southern Kuskokwim and Togiak Bays for both survey years (Fig. 2). In 1997, *G. pistilliger* were caught in 60% of the trawls <50 m (n=86 for each year), compared with 51% in 1998. The 1997 CPUE ranged from 0.19 to 101, with a mean of 15.81 (SD=22.78); the population estimate for

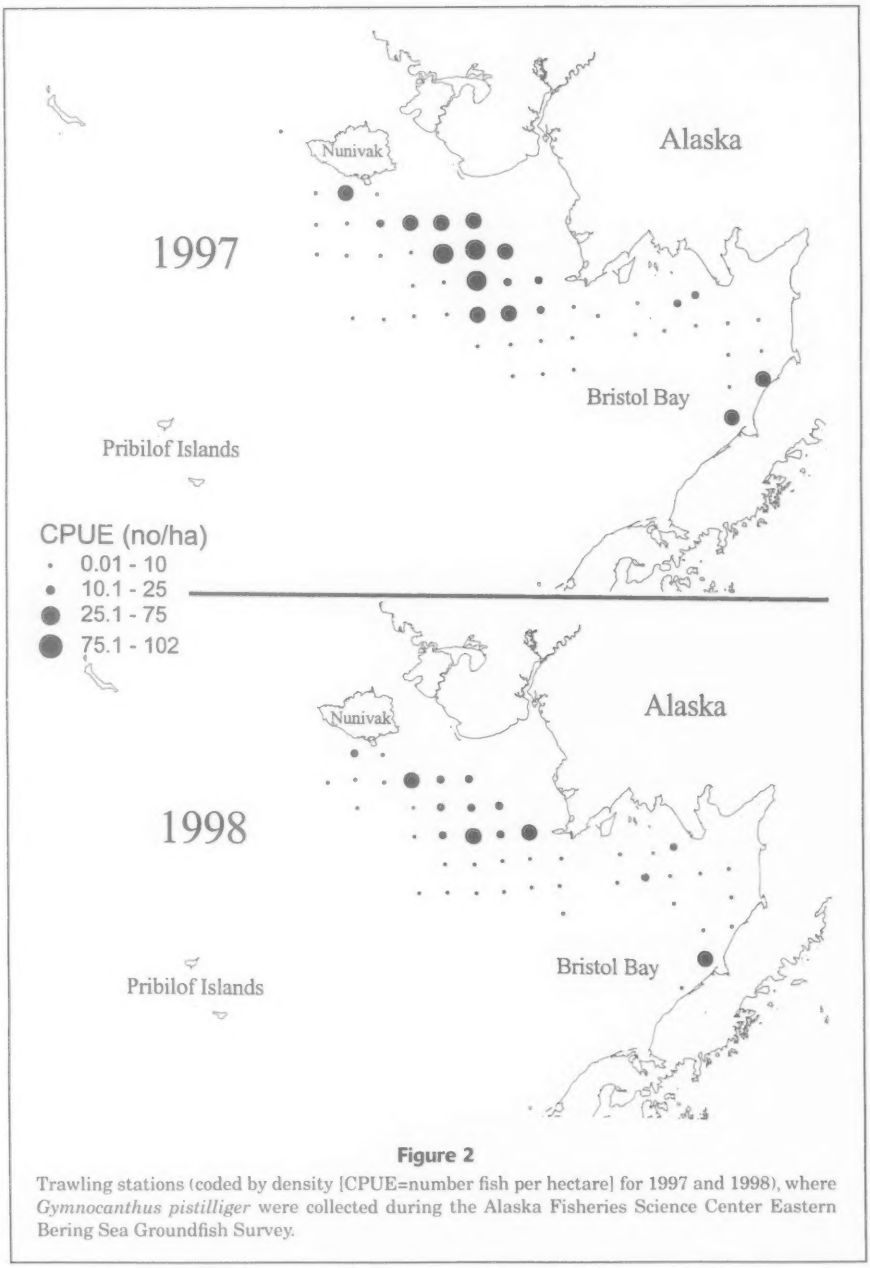

Figure 2

Trawling stations (coded by density [CPUE=number fish per hectare] for 1997 and 1998), where *Gymnocanthus pistilliger* were collected during the Alaska Fisheries Science Center Eastern Bering Sea Groundfish Survey.

the entire survey area was 110.24 million fish and the biomass estimate was 4254 metric tons (t). The 1998 CPUE ranged from 0.1 to 55 with a mean of 7.37 (SD=5.23); the population estimate was 51.70 million fish and the biomass estimate was 1956 t.

The distribution of females and males differed by depth (Fig. 3) with the proportion of females decreasing with depth. Catch rates at depth indicated that *G. pistilliger* inhabited nearshore areas and were most abundant in the shallowest depths covered by this survey (Fig. 4).

Trawling in Kuskokwim Bay and Togiak Bays resulted in mean CPUEs of 6 and 24 for each bay, respectively (n=9 trawls per bay, CPUEs of 1 to 17, SD=5.54 for Kuskokwim Bay; CPUEs of 1 to 79, SD=30.32 for Togiak Bay). During

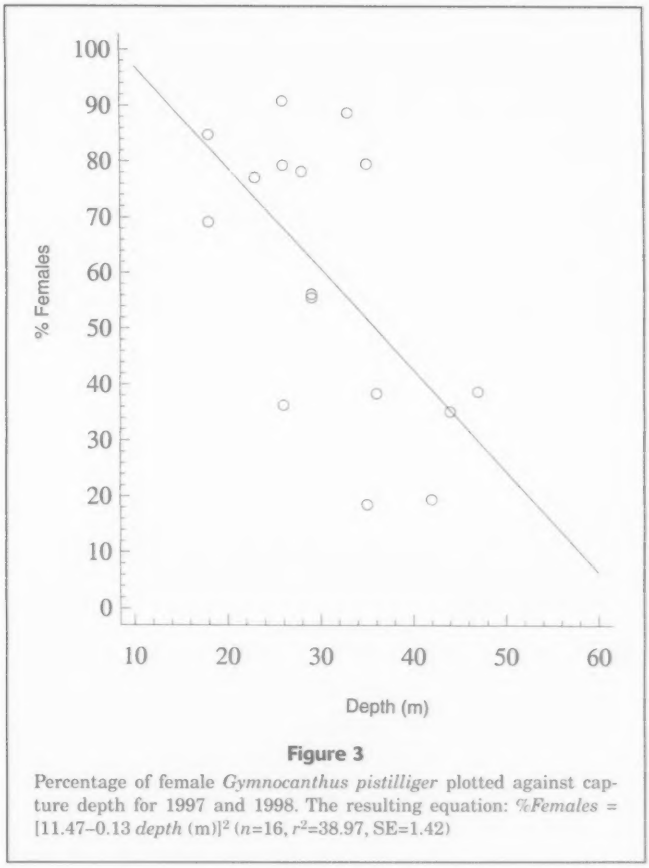

Figure 3

Percentage of female *Gymnocanthus pistilliger* plotted against capture depth for 1997 and 1998. The resulting equation: $\%Females = [11.47–0.13\ depth\ (\mathrm{m})]^2$ (n=16, r^2=38.97, SE=1.42)

these years, catches peaked in Togiak Bay (CPUEs of 71 to 79) at some of the shallowest depths trawled (13–15 m). Trawls conducted in Togiak Bay again in 1995, during late May, resulted in densities up to 249 at 19.8 m in depth (n=28 trawls, CPUEs from 4 to 249, $\bar{x}$=65.68, SD=74.68, depth range: 4–30 m).

Age and growth

A von Bertalanffy growth curve was fitted to pooled length-at-age data for 1997b and 1998 and analyzed separately for males and for females (Fig. 5). The growth models were the following:

males $L_t = 165.5\ [1-e^{-0.375299\,(t\,+\,0.0704311)}]$
(n=395, r^2=0.78, SE=8.08);

females $L_t = 223.8\ [1-e^{-0.228048\,(t\,+\,0.226626)}]$
(n=595, r^2=0.84, SE=9.85).

Females grew faster than males, and by three years of age, a difference in length at age was established (Fig. 5). Females reached >200 mm TL and a maximum age of 9 years; males reached 160 mm and a maximum age of 10 years.

Age groups from 1997 consisted of 2- to 10-year-old fish; the strongest age group was 4 years (>50% of individuals) and there were large groups of 2- and 3-year-old fish. In 1998 however, ages ranged from 3 to 9-year-old fish. The strongest age group (>50% of individuals) was 5 years. Two-year-old fish were absent (Fig. 6). Length-frequency histograms (Fig. 7) for 1997 and 1998 male and female *G. pistilliger* show the age modes as well as the age groups that were absent in 1997 and 1998.

Weight-length relationships for males and females and between years showed no significant difference (P>0.05) and were pooled for analysis (Fig. 8). The pooled weight-length equation was statistically significant (P<0.01, r^2=0.97, n=992):

$$TFW\ (\mathrm{gm}) = 2.40317 \times 10^{-6} TL\ (\mathrm{mm})^{3.30692}.$$

Ovaries were not developed in June when fish were collected; few large females contained residual eggs from the previous spawning. The GSI ranged from 0.5% to1.9% for fish collected from 1997 (females n=108, 70–190 mm TL).

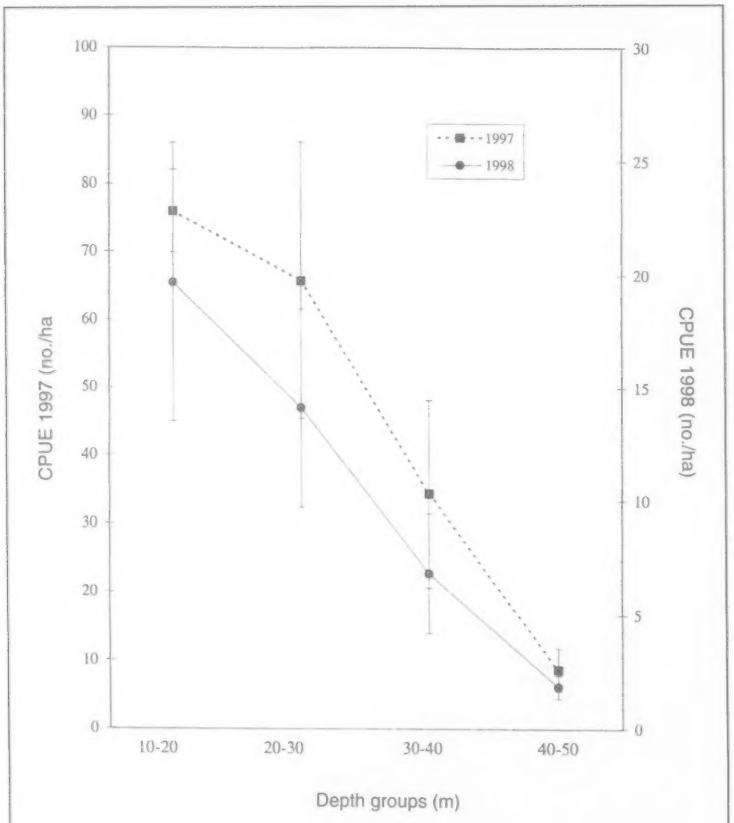

Figure 4

Mean CPUE (number fish per hectare) and standard error bars of *Gymnocanthus pistilliger* by 10 m depth groups for 1997 and 1998. Survey ranged from 15 to 178 m in depth. (1997: n=2, 12, 15, 21; 1998: n=2, 11, 15, 13 for the four depth groups, respectively).

Diet

A total of 32 different prey items were identified from 93 stomachs of fish collected in 1997 (Table 1). Frequency of occurrence analysis indicated that gammarid amphipods and polychaete worms were the most common prey items; crangonid shrimp and bivalves were encountered less frequently. Similarily prey total count indicated that gammarid amphipods were the most numerous prey items encountered but no other single item was found in large numbers. Crangonid shrimp predominated by total weight; Pacific sandlance *(Ammodytes hexapterus),* gammarid amphipods, and polycheates were secondarily important and were of approximately equal weight.

The relation between fish size and diet composition showed a shift from predominantly small benthic amphipods to increasingly larger prey items, such as crangonid shrimp and fish with increased fish TL (Fig. 9). Total diet weight proportion showed similar trends; crangonid shrimp and fish became more important and gammarid amphipods decreased in diet weight proportion as fish increased in TL (Fig. 10).

Discussion

Distribution

Gymnocanthus pistilliger is abundant in the spring to early summer (May and June) near the mouth of Kuskokwim and Togiak Bays and throughout the shallow areas of Bristol Bay. This area is characterized by relatively shallow water (<50 m) and has a sandy to muddy bottom (McDonald et. al, 1981). The Togiak River and Kuskokwim River discharge large amounts of fresh water into the shallow estuarine environment creating fluctuating tem-

peratures and salinities; thus, during winter the entire area may be covered in thick ice sheets. *Gymnocanthus pistilliger* may move in and out of the shallow local bays seasonally to sustain a suitable habitat. However the nearshore distribution was difficult to assess for *G. pistilliger* from the present study owing to limited sampling in very shallow coastal waters and single season collections. The timing of spawning movements, however, may significantly affect population estimates if the species moves between depths seasonally and may help to explain a 50% decline in fish from 1997 to 1998. Although water temperature is often associated with fish movements, there was no significant difference between the means (t-test P=0.18) in bottom water temperatures in the survey area <50 m in depth for the two years sampled (1997, $\bar{x}$=4.22°C, SD=1.88; 1998, $\bar{x}$=4.48°C, SD=0.87).

Vdovin et al. (1994) suggested that *G. pistilliger* remains within shallow water and except for spawning, probably remains in the nearshore area most of the year. Spawning migrations in winter resulted in both sexes aggregating in deeper bay areas of Peter the Great Bay (Vdovin et al., 1994); however, the proportion of females increased with increasing depth (a depth range of 80 to 110 m was maintained during spawning) (Tokranov, 1987; Vdovin et al., 1994).

If Bristol Bay populations are similar to Peter the Great Bay populations, then at the time of capture (June) *G. pistilliger* has already spawned and dispersed in the nearshore areas. Females probably migrate to join the males in the deeper part of Bristol Bay (around 50 m depth) during late winter to early spring to spawn, although it is unlikely that Bristol Bay populations reach the spawning depths of populations in Peter the Great Bay. Distributional data from Alaska indicate that *G. pistilliger* are rarely found deeper than 50 m, except occasionally in coastal areas of the Gulf of Alaska (Hoff, unpubl. data).

Age and growth

Age data gathered from otoliths suggest that *G. pistilliger* is short lived (to 10 years), the females exhibit faster growth, and that this species reaches a maximum size of 205 mm for females and 160 mm for males. The age structure of western Bering Sea populations has shown older populations than those for Bristol Bay (a strong mode from 7 to 9 years (range 3–13 years) and a larger maximum size of 270 mm TL for females and 220 mm TL for males (Tokranov, 1987). Length-at-age data for fish collected off Kamchatka (Tokranov, 1987) were similar to those reported in the present study, suggesting that similar aging techniques were used and similar growth rate estimates were calculated for the two populations of *G. pistilliger*. Therefore, different size composition and age groups for eastern Bering Sea and western Pacific populations appear real.

The ovaries from females collected in June from Bristol Bay were deflated and a few large females contained residual eggs from a previous spawn. Wilson (1973) stated that *G. pistilliger* spawn in spring but provided no evidence for this. Ovaries collected from eastern Bering Sea populations in June of 1997 suggest that *G. pistilliger* is a late winter to early spring spawner. Tokranov (1987) reported that *G. pistilliger* spawn in winter, are single batch spawners in shallow waters, and produce adhesive eggs.

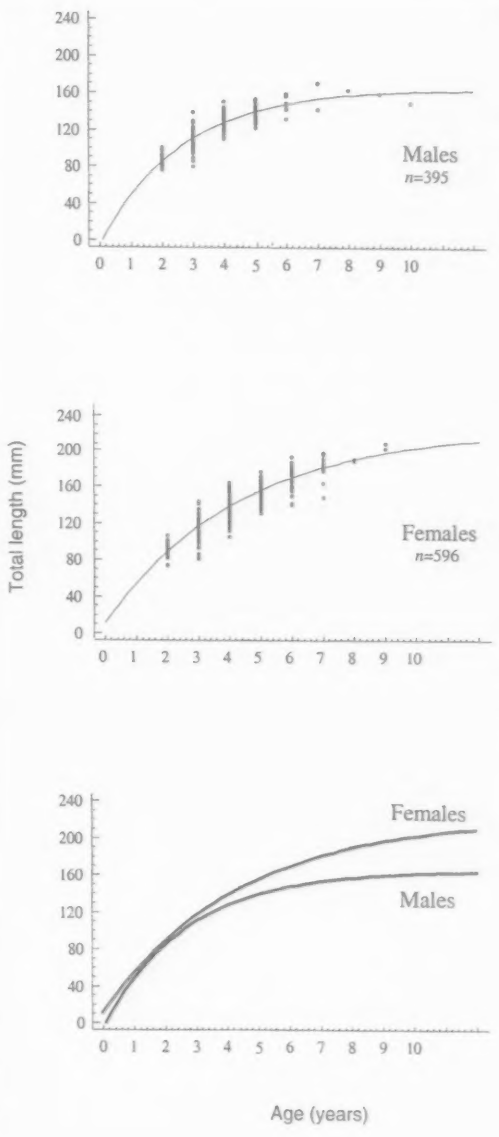

Figure 5

Von Bertalanffy growth curves and individual data for male and female *Gymnocanthus pistilliger* collected during 1997 and 1998, combined with curves plotted together for comparison. Length-at-age data were gathered from sagittal otoliths by the break-and-burn method.

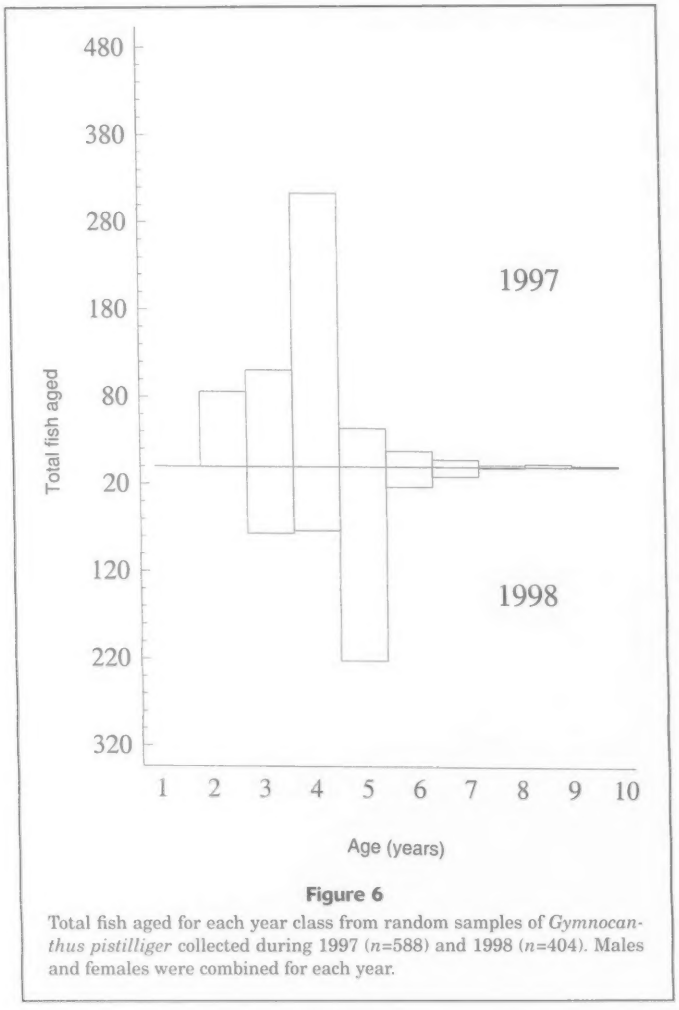

Figure 6

Total fish aged for each year class from random samples of *Gymnocanthus pistilliger* collected during 1997 (n=588) and 1998 (n=404). Males and females were combined for each year.

Diet

Gymnocanthus pistilliger preys upon benthic amphipods, polychaetes, crangonid shrimp, and fish. A diet shift from amphipods to shrimp and fish with increased body size represents the sculpin's ability to capture and ingest larger prey items with increased body size, an ability that lessens the likelihood of intraspecific competition and increases efficiency in feeding.

Tokranov (1985) reported on the diets of *G. pistilliger* from off the western coast of the Kamchatka Peninsula. He found diets consisted mainly of polychaete and *Echiurus* (~70% frequency and weight) and amphipods (contributing little to the diet). *Gymnocanthus pistilliger* from Kamchatka increasingly consumed mollusks, decapods, and juvenile capelin as it grew, and polychaetes and *Echiurus* decreased as important items in the diet. Tokranov (1985) also found a shift to larger prey items with increasing fish size.

Commercially important flatfish also use shallow waters in Bristol Bay as spawning and nursery grounds (Fadeev, 1968; Grigorev and Fadeev, 1995). The diet composition of *G. pistilliger* overlaps with that of flatfish species, such as *Limanda aspera* (yellowfin sole), *Limanda proboscidea* (long-head dab), *Pleuronectes bilineatus* (rock sole), and *Pleuronectes quadrituberculatus* (Alaska plaice), where competitive interactions may occur. These flatfish diets also consist of benthic amphipods, polychaetes, and *Echiurus* (>50% by weight) (Livingston et al., 1986; Brodeur and Livingston, 1988; Corcobado-Onate, 1991; Lang et al., 1995). However, Holladay and Norcross (1995) found that these flatfish species exhibit a diverse diet (10–57 groups) and show diet preferences based on substrate. Dietary shifts such as these may lessen the likelihood of prey competition in densely populated areas such as Bristol Bay.

Gymnocanthus pistilliger is also potentially an important resource to larger predators because of its small size

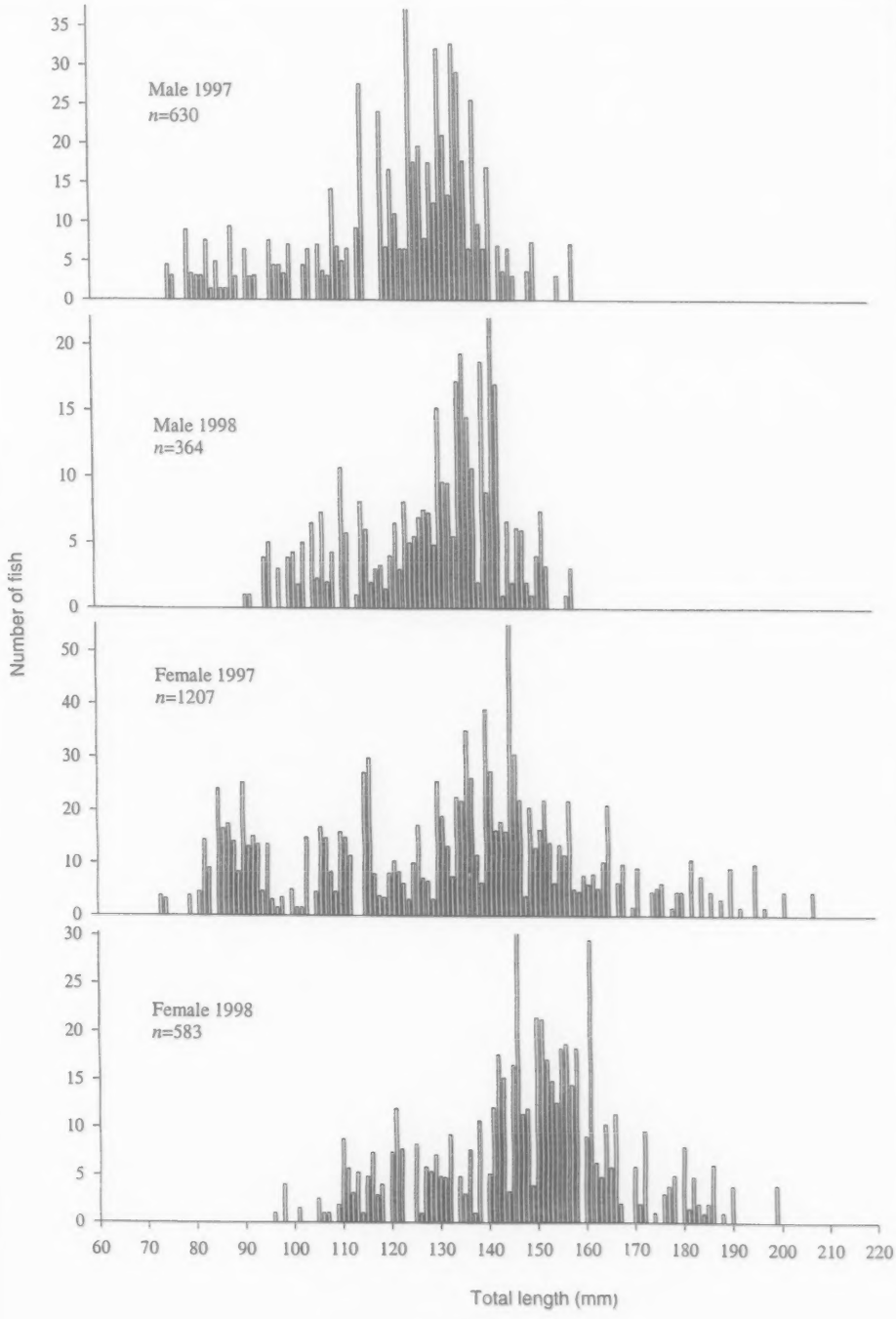

Figure 7

Length frequencies for male and female *Gymnocanthus pistilliger* for 1997 and 1998.

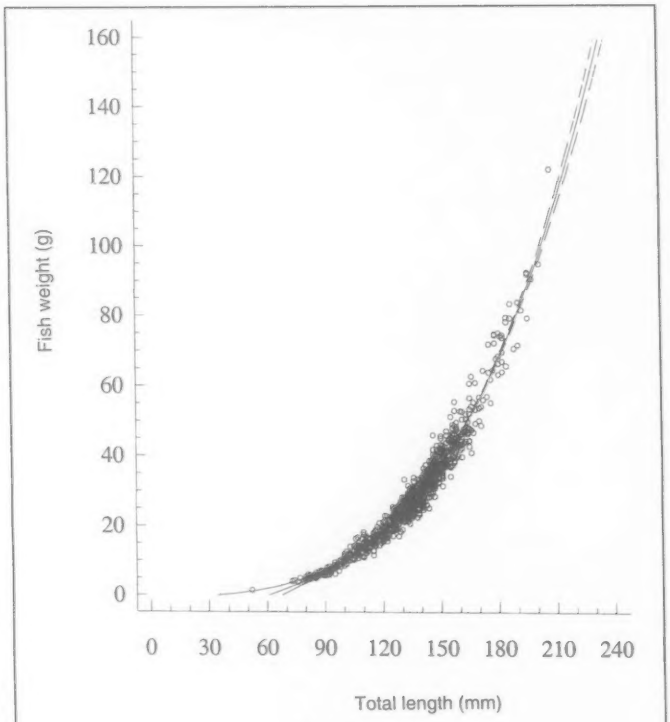

Figure 8

Weight-length relationship for *Gymnocanthus pistilliger* for 1997 and 1998 males (n=394) and females (n=596) combined. Solid line is the fitted model, dashed line represents the 95% confidence intervals. (P<0.01, SE=0.097).

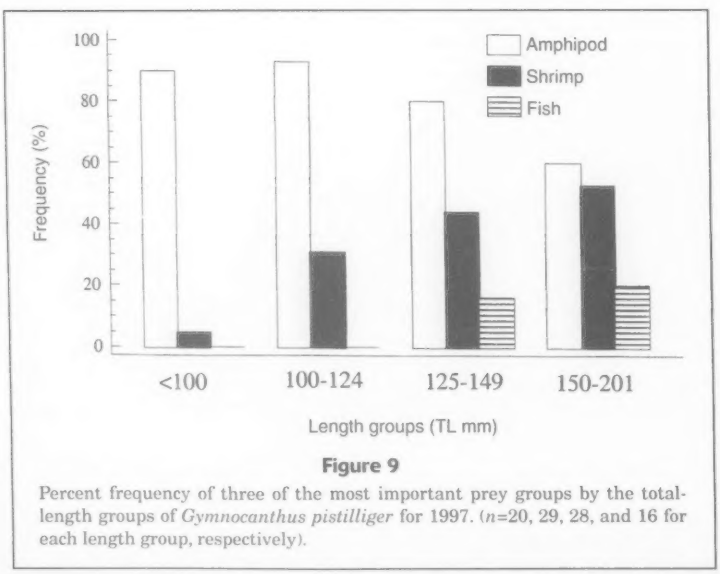

Figure 9

Percent frequency of three of the most important prey groups by the total-length groups of *Gymnocanthus pistilliger* for 1997. (n=20, 29, 28, and 16 for each length group, respectively).

and relative abundance. Pacific cod from Bristol Bay have been found to occasionally feed on *G. pistilliger*.[1] Bearded seals, *Erignathus barbatus*, whose distribution overlaps with *G. pistilliger*, consume sculpin species (>80% by volume) (Lowry et al., 1980) and may exploit *G. pistilliger*. However, many feeding studies on seals do not document which species of sculpins were found as prey items.

Gymnocanthus pistilliger is an abundant, short-lived cottid species occurring in shallow waters of the Bristol Bay area. Owing to its great abundance, it may make up an important part of the biomass resource in its range. There are distinct biological differences, such as male-to-female ratios with depth, maxi-

[1] Buckley, T. 1998. Personal commun. Alaska Fisheries Science Center, National Marine Fisheries Service, NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115.

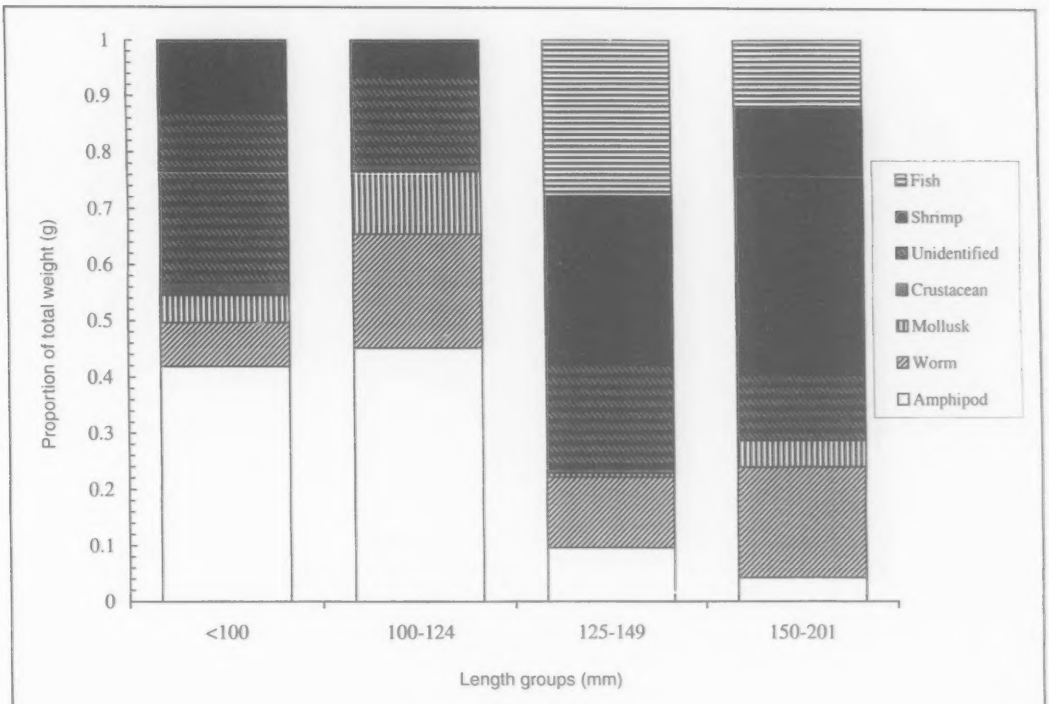

Figure 10

Proportion of the total weight of all prey groups by the total-length groups of *Gymnocanthus pistilliger* for 1997. (*n*=20, 29, 28, and 16 for each length group, respectively).

mum depth, maximum age and size, and diet preferences between western and eastern North Pacific populations. The eastern Bering Sea and Kamchatka shelf habitats have different currents, salinities, sediment types, shelf area, and temperatures (Pavlov and Pavlov, 1996) and these different oceanographic features may be reflected in the local adaptation patterns of *G. pistilliger* in this area.

Smith et. al (1997) reported on the biology of *Gymnocanthus tricuspis,* a congener of *G. pistilliger,* which is abundant in the Chukchi Sea and Norton Sound, Alaska (Allen and Smith, 1988). The two species of *Gymnocanthus* are very similar and probably occupy the same ecological niche in different environments. Smith et. al (1997) reported similar ages up to 9 years of age and similar densities and interannual variations in populations of *G. tricuspis* as were found for *G. pistilliger*. The ecological importance of *Gymnocanthus* throughout its range is not well understood but undoubtedly significant because of its high abundance and role as prey and competitive predator.

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Age, growth, mortality, and reproduction of red porgy, *Pagrus pagrus*, from the eastern Gulf of Mexico

Peter B. Hood

Florida Marine Research Institute
Florida Department of Environmental Protection
100 Eighth Avenue SE, St. Petersburg, Florida 33701-5095
Present address: Gulf of Mexico Fishery Management Council
3018 U.S. Hwy. 301 North, Suite 1000
Tampa, Florida 33619-2266
E-mail address: peter.hood@gulfcouncil.org

Andrea K. Johnson

College of Veterinary Medicine
North Carolina State University
4700 Hillsborough St.
Raleigh, North Carolina 27606

Abstract–The red porgy (*Pagrus pagrus*) is an important component of the Gulf of Mexico reef-fish fishery, yet little information is available on this species's life history. We sampled 877 red porgy (194–489 mm TL) from the eastern Gulf of Mexico during 1995 and 1996 to assess their age structure, growth, mortality, spawning season, size and age at maturity, and batch fecundity. The average length of males was significantly greater than that of females, and the overall sex ratio (1:1.6 in favor of females) was significantly different from 1:1. Marginal-increment analysis indicated that one opaque ring is formed on red porgy otoliths during the late spring or early summer of each year. Ages ranged from 1 to 17 years, and most fish were 3 and 8 years old. Von Bertalanffy growth model parameters were L_∞=459 mm TL, K=0.111/yr, and t_0=–6.6 years for all aged fish. Growth rates in our study were lower than those in previous studies of Gulf of Mexico red porgy—perhaps the result of size-selective fishing. Pooled estimates of total instantaneous mortality were 0.62–0.87/yr based on recreational landings data and 0.54/yr based on commercial landings data. Red porgy are protogynous hermaphrodites. The length and age at which males composed 50% of the population was 345.5 mm TL and 5.3 years. Few immature females were observed in our collections (n=10). All females greater than 302 mm TL and age 4 were mature. Red porgy spawn during the winter and spring, and ripe females were caught from January to April.

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The red porgy, *Pagrus pagrus*, occurs in the eastern Atlantic from the British Isles south to Angola and in the western Atlantic from New York to Argentina (Manooch and Hassler, 1978; Randall and Vergara, 1978). In the Gulf of Mexico (GOM), red porgy are usually found near hard-bottom areas off the west-central Florida coast and the Florida Middle Ground, and the Flower Garden Banks off Texas (Smith et al., 1975; Nelson, 1988). Studies of reef habitat along the southeastern United States indicate that red porgies are most common over inshore live-bottom habitats and over shelf-edge, rocky-rubble, and rock outcrop habitats (Grimes et al., 1982; Barans and Henry, 1984; Chester et al., 1984; Sedberry and Van Dolah, 1984).

Most red porgy caught in the GOM are landed in Florida. From 1986 to 1991, an average of 83.6% of the commercially caught and 76.7% of the recreationally caught red porgy were landed there (Goodyear and Thompson[1]). Red porgy are an important component of the Florida west coast commercial reef-fish fishery and rank thirteenth in total weight of reef fish landed in this area (Goodyear and Thompson[1]). In Florida commercial landings data, red porgy are not distinguished from other porgies. However, assuming that red porgies made up 50% of all porgies landed (Goodyear and Thompson[1]), the combined west coast 1995 and 1996 Florida landings of this species were estimated at 0.5 million pounds and had an estimated dockside value of $487,000 (Marine Fisheries Information System[2]). Over the same period, an estimated 242,000 red porgy were landed by anglers in Florida (Marine Recreational Fishery Statistics Survey[3]), 80% by charter boats or headboats (Goodyear and Thompson[1]).

Currently there are no regulations on red porgy harvest in the GOM. Fishery managers are concerned that the harvest of reef-fish species, such as red porgy, may increase if the fishery shifts effort from red snapper to these species because of increasing restrictions

[1] Goodyear, C. P., and N. B. Thompson. 1993. An evaluation of data on size and catch limits of red porgy in the Gulf of Mexico. Contribution report MIA-92/93-67. National Marine Fisheries Service, Southeast Fisheries Center, Miami Laboratory, Miami, FL.

[2] Marine Fisheries Information System. 1997. Unpubl. data. Florida Fish and Wildlife Conservation Commission, 100 Eighth Avenue SE, St. Petersburg, FL 33701-5095.

[3] Marine Recreational Fishery Statistics Survey (MRFSS). 1997. Unpubl. data. Fisheries Statistics Division, National Marine Fisheries Service, Department of Commerce, Silver Springs, MD 20910.

on the GOM red snapper fishery (Anonymous[4]). The red porgy fishery shifted from a predominately recreational fishery to a predominately commercial fishery between 1988 and 1991 (Goodyear and Thompson[1]). Owing to these changing dynamics within the red porgy fishery, the Reef Fish Stock Assessment Panel of the Gulf of Mexico Fishery Management Council recommended that age, growth, and reproduction studies be initiated for future stock assessments (Anonymous[4]). Red porgy are protogynous hermaphrodites and may be more susceptible to overfishing than gonochoristic reef-fish species such as snappers if size-selective fishing reduces the number of males available for spawning and thus limits the amount of sperm available for fertilization (Bannerot et al., 1987; Koenig et al., 1996).

Existing age and growth data for this species in the GOM are inadequate. Nelson (1988) used scales to age red porgy collected from the Flower Garden Banks off Texas in the early 1980s and reported a maximum age of 6 years. This value is much lower than maximum ages reported from other regions. Maximum ages, determined from scales, whole otoliths, and sectioned otoliths have ranged from 13 to 18 years (Manooch and Huntsman, 1977; Vassilopoulou and Papaconstantinou, 1992; Pajuelo and Lorenzo, 1996; Harris and McGovern, 1997; Vaughan[5]). Nelson (1988) suggested that the reason he did not observe fish as old as those observed by Manooch and Huntsman (15 years; 1977) was that fishing had removed older fish from the GOM. However, mortality rates in the South Atlantic Bight (SAB) are now greater than those reported by Nelson (1988) for the GOM, and SAB fish as old as age 18 have recently been reported by Vaughan.[5]

Little information is available on the reproductive biology of red porgy in the GOM. Female red porgy begin to transform into males at 221 mm fork length; however, the length at which females begin to mature in the GOM is unknown because the smallest female sampled by Nelson (1988) was 272 mm fork length and all females that he examined were mature. Spawning occurs in the winter and spring in the GOM, as has been reported for the SAB, Canary Islands, and Mediterranean Sea (Manooch, 1976; Nelson, 1988; Vassilopoulou and Papaconstantinou, 1992; Pajuelo and Lorenzo, 1996), although Ciechomski and Weiss (1973) reported, on the basis of larval collections, that red porgies may spawn in the Argentine Sea during the summer (December and January).

Basic life-history information is needed for use in assessments of red porgy stocks in the GOM. Although Nelson (1988) examined red porgy age, growth, and reproduction in the GOM; his study was limited by area (Flower Garden Banks off Texas), sample size (n=126), and aging structure (scales). Accurate ages are needed to develop growth models, develop age-length keys, and estimate total mortality. In addition, the annual periodicity of ring deposition in otoliths has not been validated for red porgy in the GOM. With the increasing reliance on estimates of spawning-potential ratios to describe a stock's condition, information on maturation schedules and sex ratios are also needed. The purpose of our study was to age eastern GOM red porgy accurately in order to develop age-length keys and growth models, to construct catch curves for deriving estimates of total mortality, and to describe the reproductive biology of this species.

Methods

Collections

Eastern GOM red porgy were sampled from headboat and commercial catches between October 1995 and September 1996. Total length (TL), fork length (FL), and standard length (SL) were measured to the nearest millimeter. Whole weight and gutted weight were measured to the nearest gram (g). The relationships between lengths, weights, and $\log_{10}$-transformed total lengths and weights were determined by least-squares regression (SAS Institute, Inc., 1985). Male and female regression lines of $\log_{10}$-transformed total lengths and weights were compared by using analysis of covariance (Snedecor and Cochran, 1971). Length-frequency distributions were compared by sample source and by sex by using the Kolmogorov-Smirnov test for goodness of fit (Sokal and Rohlf, 1981). All length data are reported as total length unless stated otherwise.

Age, growth, and mortality

Thin sections of otoliths (sagittae) were used to determine the ages of fish. Otoliths were removed and stored dry in culture wells. The left otolith was serially sectioned across its anterior-posterior midpoint at 0.5-mm intervals by making a transverse cut with an Isomet diamond saw. Mounted sections were placed on a black field, illuminated with reflected light, and examined with a binocular dissecting microscope. The magnified images of otolith sections were transmitted by means of video camera to a video monitor. The number of opaque zones and the radial measurements from the core to the last opaque zone and to the edge of the otolith (otolith radius, Fig. 1) were recorded from the monitor by using a computer-driven, data-acquisition software package (Optimas Corp., 1996). Marginal increments were measured as the distance between the last opaque zone and the edge of the otolith.

To determine if zone counts were repeatable between investigators, two readers independently examined sectioned otoliths collected from fish collected during July and August 1996 (n=241). After the first reading, readers examined the sections together and compared zone counts to form a consensus about what constituted a zone. The two readers then re-examined the sectioned otoliths independently, and counts were compared again. Because agreement between

[4] Anonymous. 1993. Final report of the reef fish stock assessment panel. Gulf of Mexico Fishery Management Council, 3018 U.S. Highway 301 N, Suite 1000, Tampa, FL 33619-2266.

[5] Vaughan, D. S. 1999. Population characteristics of the red porgy *Pagrus pagrus* from the U.S. Southern Atlantic Coast. Report prepared for the South Atlantic Fishery Management Council. National Marine Fisheries Service, Beaufort Laboratory, 101 Pivers Island Road, Beaufort, NC 28516

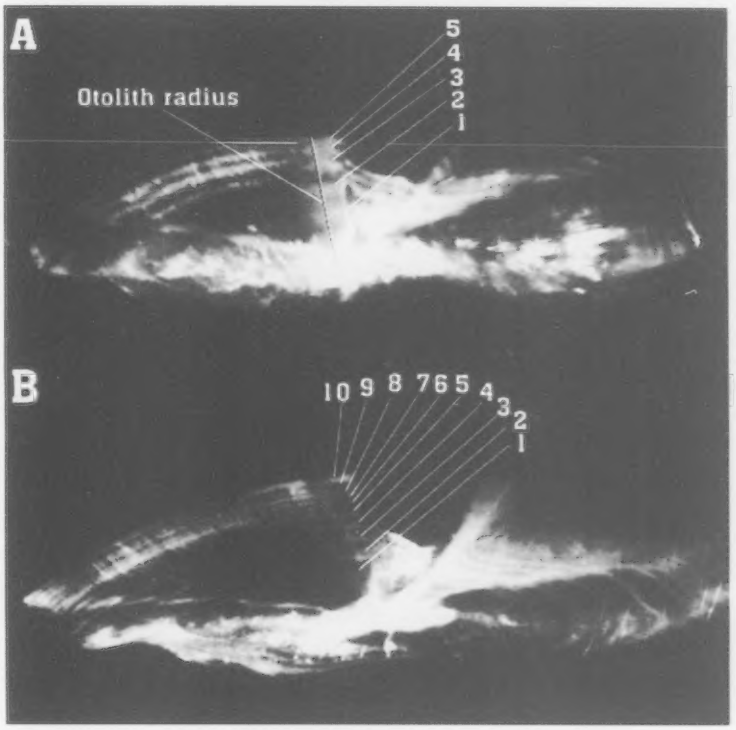

Figure 1

Sectioned sagittae from (**A**) a 5-year-old (345-mm-TL) and (**B**) a 10-year-old (485-mm-TL) eastern Gulf of Mexico red porgy. The 5-year-old fish was caught in September 1996, and the 10-year-old fish was caught in April 1996.

readers was high (86%) for the second readings, one reader read the remaining otoliths to determine age. Each of the remaining otolith sections was read three times, and annulus counts were accepted for ages only if at least two of the three separate readings were the same. Age was considered to be the count with the highest frequency of occurrence. To validate annulus periodicity, marginal increments and their medians were plotted by month for each age and compared for consistent temporal patterns.

Age in years was estimated as the number of opaque rings; therefore, length at age included any growth that occurred after the last opaque ring was formed. Length at age between sampling sources was compared by using an unbalanced two-way analysis of variance (SAS Institute, Inc., 1985). Mean observed length at age was calculated for males, females, and for all aged fish. Age and length data were fitted to a von Bertalanffy growth model with nonlinear regression (SAS Institute, Inc., 1985). We calculated an adjusted r^2 for the resulting curve by using methods described by Helland (1987).

We used age-frequency data from this study to estimate mortality rates from Florida commercial and recreational length data for Florida. Because the number of red porgy measured by the Trip Interview Program[6] and MRFSS[3] were low, we pooled the data from the most recent years for which data were available. Length data from commercial landings were obtained from the TIP[6] from 1992 to 1994 and in 1996. Length data from recreational landings were obtained from the MRFSS[3] and the National Marine Fisheries Service's Headboat Survey[7] and were pooled for years 1990–1996. Because red porgies are protogynous hermaphrodites, we pooled sexed and unsexed fish to generate the catch curves. Instantaneous mortality and survivorship rates were estimated by the Chapman-Robson method (Youngs and Robson, 1978). Age at full recruitment was estimated from the catch curve as being one year older than the age with the greatest catch.

[6] Trip Interview Program (TIP). 1997. Unpubl. data. Florida Fish and Wildlife Conservation Commission, 100 Eigth Avenue, SE, St. Petersburg, FL 33701-5095.

[7] National Marine Fisheries Service Headboat Survey. 1999. Unpubl. data. Beaufort Laboratory, 101 Pivers Island Rd., Beaufort, NC 28516-9722.

Reproduction

Reproductive analyses were based on gonad weights and a histological examination of gonadal tissue. Fish sampled were put on ice soon after capture, and we sampled fish within 36 hours after their capture by the recreational fishery and 10 days after their capture by the commercial fishery. Whole gonads were weighed to the nearest 0.1 g. Some fish were gutted before they were landed. If a portion of gonad was present, it was removed for histological preparation; if none was present, the sex of the fish was listed as unknown. Gonads were fixed in 10% buffered formalin for approximately one week, rinsed in water, and then transferred to 70% ethanol. We removed a sample of tissue from the middle of the preserved gonad and embedded it in paraffin. Several 5.0-µm sections were serially cut from the sample, stained with Harris's haematoxylin, counterstained with eosin (Humason, 1972), and examined under a compound microscope to determine sex and developmental state of the gonads. For ovaries, we staged oocytes as being primary growth, cortical alveoli, or vitellogenic oocytes, or as mature oocytes by using criteria developed by Moe (1969), Wallace and Selman (1981), and West (1990). The frequency of occurrence of oocyte developmental stages (including atretic bodies and postovulatory follicles) was tabulated for approximately 300 oocytes from each ovary by using a computer-driven data-acquisition software package (Optimas Corp., 1996). Mature ovaries were distinguished from immature ovaries by the presence of atretic bodies, advanced oocyte development stages (vitellogenic or mature oocytes), or both. Testes were assigned to development classes (Table 1) by using a modified classification scheme developed from Hyder (1969) and Moe (1969). Transitional males (individuals with gonads in transition from ovaries to testes) were identified according to the criteria of Sadovy and Shapiro (1987).

Sex ratios for all sexed fish were compared for significant differences from 1:1 by using the chi-square test (Snedecor and Cochran, 1971). The length and age at which 50% of the population consisted of males was estimated by fitting a logistic curve to length and age data with sex as a binary response equal to zero for females and to one for males. The curves were fitted to the data by using nonlinear regression (Jandel Corp., 1992).

Reproductive seasonality was determined by examining the monthly changes in gonad stages, the monthly distribution of oocyte stages, and the monthly changes in the gonosomatic index (GSI). The GSI was calculated by using the following equation:

$$GSI = \text{gonad weight}/(\text{whole weight} - \text{gonad weight}).$$

Table 1

Development classes for testes of red porgy.

Classes	Testes
Transitional	Massive atresia of oocytes. Spermatogonia, spermatocytes, and (or) spermatids developing in lumen of testicular lumen. Tailed sperm may be present.
Resting	Mostly spermatogonia and spermatocytes present in the central lobules. Free spermatozoa in the lumen of the lobule, and brown bodies (Grier, 1987) may be present.
Developing	Mostly spermatocytes and spermatids present in the central lobules, free spermatozoa in the lumen of the lobule.
Ripe	Mostly spermatozoa found in the central lobules and in the lumen of the lobule; all or later stages of spermatogenesis occurring in the peripheral lobules.
Spent	Few free spermatozoa in the lumen of the lobule; early stages of spermatogenesis in the peripheral lobules.

Results

Collections

We sampled 877 red porgy that ranged from 194 to 489 mm in length. Although we did not record the locations where fishermen caught their fish, most fishing effort was directed in the Florida Middle Ground and off west central Florida. Most fish (92%) were in length classes between 251 and 400 mm long and had a modal length class of 326–350 mm (Fig. 2). Relationships between lengths, between whole weight and gutted weight, and between TL and weight are shown in Table 2. Male and female data were pooled for the weight-length relationship because sex-specific regression equations were not significantly different (ANCOVA, $P>0.05$). Most of the fish sampled were from the recreational fishery ($n=601$), and they ranged in length from 205 to 455 mm (Fig. 2). Fish from the commercial fishery ($n=276$) ranged from 265 to 489 mm (Fig. 2). The mean length of recreationally caught fish (321 mm, SE=40) was significantly less than the mean length of commercially caught fish (350 mm, SE=40; t-test, $P<0.001$). The length-frequency distributions for commercially and recreationally caught fish were significantly different ($D=0.287$, $P<0.001$). Males ($n=331$) ranged in length from 248 to 470 mm and females ($n=456$) from 205 to 455 mm (Table 3). The mean length of males (341 mm, SE=36.3) was significantly greater than that of females (316.2 mm, SE=40.5; t-test, $P<0.001$). The length-frequency distributions for males and females were significantly different ($D=0.317$, $P<0.001$). The largest fish examined (489 mm) had been gutted; therefore the sex of the specimen was unknown.

Age, growth, and mortality

Under reflected light, alternating opaque (white) and translucent (dark) zones were evident in red porgy otoliths (Fig. 1). Two readers examined a subsample of 241 otoliths, and 50% of their readings were in agreement. Most of the disagreements (71%) differed by only one

Table 2

The linear relationships among lengths, among weights, and between weight and length, and the logistic proportion of males by age and total length for red porgy from the eastern Gulf of Mexico. SL = standard length (mm), FL = fork length (mm), TL = total length (mm), WT = whole weight (gm), GWT = gutted weight (gm). n = the number of fish sampled, and the standard error is given in parentheses.

$Y = a + bX$					
Y	X	n	a	b	r^2
SL	FL	876	−5.3 (1.4)	0.89 (0.005)	0.97
SL	TL	869	−10.1 (1.6)	0.78 (0.005)	0.97
FL	SL	876	13.0 (1.5)	1.09 (0.005)	0.97
FL	TL	867	−4.9 (1.0)	0.87 (0.003)	0.99
TL	SL	869	24.5 (2.0)	1.24 (0.01)	0.97
TL	FL	867	8.9 (1.1)	1.13 (0.004)	0.99
WT	GWT	121	6.0 (3.4)	1.05 (0.008)	0.99
$\log_{10}WT$	$\log_{10}TL$	572	−4.51 (0.053)	2.86 (0.216)	0.97
$\log_{10}GWT$	$\log_{10}TL$	272	−4.45 (0.08)	2.82 (0.32)	0.97
$Y = 1/(1+e^{(a(x-b))})$					
Proportion male	*Age*	781	−0.703 (0.067)	5.332 (0.118)	
Proportion male	*TL*	784	−0.017 (0.002)	345.5 (5.1)	

zone. A second independent reading of the subsample by both readers resulted in a higher agreement rate of 86% and indicated that both readers were consistently identifying the same features as opaque zones. Of 877 sectioned otoliths examined, 852 (97%) could be assigned ages. Of the otoliths that could be aged, measurements for marginal-increment analyses could not be made for 40 (4.6%) because of broken or occluded areas along the otolith radius.

Analyses of marginal-increment data for fish ages 2–10 yr suggested that opaque zones were formed once a year during the late spring to early summer (Fig. 3). Because of small sample sizes, we pooled marginal-increment data for ages 8 to 10. During the spring and early summer, the widest increments (ring formation was imminent) and the narrowest increments (ring formation was just completed) were present, indicating that rings were being formed during this period. In addition, monthly median marginal increments for ages 2–10 had a consistent yearly pattern of high median values from October to April and low values from June to August (Fig. 3).

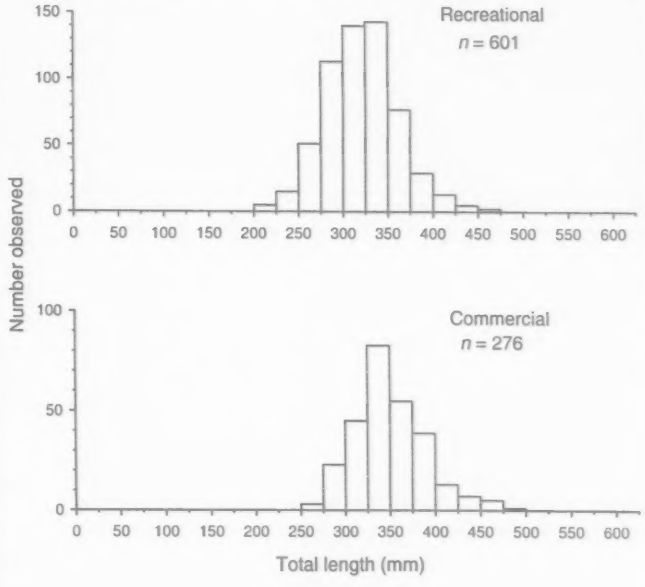

Figure 2

Total lengths of red porgy from the eastern Gulf of Mexico by sampling source.

Ages ranged from 1 to 17 years and most fish (83%) were between ages 3 and 8. No females older than 10 years were observed. Initial growth of red porgy was rapid, and fish attained a mean length of 260 mm during their second year (age 1; Table 4). Subsequent increases in length, however, were low (<40 mm/yr). Average lengths at age were not significantly different between males and females ($F_{8,741}$=1.5, P=0.155) or between sampling sources ($F_{8,817}$=0.96, P=0.462). The

estimated von Bertalanffy growth parameters (standard error) for all aged fish (n=854) were L_∞=459(31) mm, K=0.111 (0.028)/yr, and t_0=–6.6 (1.3) yr. Predicted lengths at age were similar to mean lengths at age (Table 4, Fig. 4). The adjusted r^2 for the growth model was 0.40.

Fishery-based length-frequency data were transformed into age frequencies by using age- length keys constructed from the ages of the fish in our study. Full recruitment into both the recreational and commercial fisheries occurred at age 4. Survivorship (standard error) of red porgy was estimated to be 0.42(0.001) from the headboat fishery data, 0.54(0.046) from the recreational fishery data and 0.58(0.014) from the commercial fishery data. Instantaneous mortality estimates (Z=–ln survivorship) were 0.87

Table 3

Number of males, number of females, and percentage of male red porgy in relation to the total number of sexed individuals by length and age from the eastern Gulf of Mexico.

Length (mm TL)	No. of females	No. of males	% males	Age (yr)	No. of females	No. of males	% males
<200	1	—	—	1	6	1	14.29
201–225	4	—	—	2	55	5	8.33
226–250	14	1	6.67	3	100	20	16.67
251–375	48	6	11.11	4	124	38	23.46
276–300	98	37	27.41	5	89	89	50.00
301–325	113	60	34.68	6	49	63	56.25
326–350	95	113	54.33	7	15	64	81.01
351–375	46	63	57.80	8	6	28	82.35
376–400	22	29	56.86	9	2	9	81.82
401–400	7	16	69.57	10	3	10	76.92
426–450	3	5	62.50	11+		5	100
451–475	2	1	33.33				

Table 4

Mean empirical and predicted total lengths (mm TL) of female, male, and all red porgy sampled from the eastern Gulf of Mexico. Standard error is given in parentheses, and n = number of fish examined.

	Female			Male			All fish			
Age (yr)	n	Mean empirical	Range	n	Mean empirical	Range	n	Mean empirical	Range	Predicted
1	6	253 (36.7)	194–290	1	298	—	7	260 (37.4)	194–298	262
2	55	292 (31.8)	205–363	5	311 (40.9)	285–382	61	294 (32.6)	205–382	283
3	99	288 (29.1)	230–368	20	300 (28.9)	248–350	124	291 (31.2)	220–378	302
4	122	315 (29.9)	245–402	38	318 (30.0)	258–372	171	316 (29.7)	245–402	318
5	88	337 (36.5)	265–455	87	337 (32.4)	276–435	189	339 (34.8)	265–455	333
6	48	344 (25.3)	290–405	63	346 (26.1)	300–420	134	348 (26.9)	290–426	347
7	15	360 (21.9)	330–397	62	351 (32.0)	288–425	88	357 (33.3)	288–489	358
8	6	364 (33.1)	326–415	27	340 (20.2)	295–380	38	348 (27.0)	295–425	369
9	2	410 (46.0)	377–442	9	379 (36.7)	330–450	13	388 (40.0)	330–452	379
10	3	379 (39.6)	334–407	9	407 (38.5)	348–470	18	396 (46.5)	321–470	387
11				1	405	—	4	415 (20.9)	390–436	395
12				1	397	—	2	393 (5.7)	389–397	402
13				1	393	—	1	393	—	408
14				1	389	—	2	377 (17.7)	364–389	413
15							1	445	—	418
17				1	438	—	1	438	—	426

for the headboat fishery, 0.62 for the recreational fishery, and 0.54 for the commercial fishery.

Reproduction

Red porgy are protogynous hermaphrodites. We classified 68 males (8% of the sexed fish) as transitional-sex-stage fish because of the simultaneous presence of deteriorating ovarian tissue and proliferating male tissue. We determined that the gonadal structure was delimited (Sadovy and Shapiro, 1987) because connective tissue separated testicular from ovarian tissue. Sex ratios and length and age data were consistent with monandric protogyny. The overall sex ratio of males to females was 1.0:1.6, which was significantly different from 1:1, χ^2=51.0, df=1, P<0.001). In addition, the modal length class and age of females (301–325 mm; 4 yr) were less than the modal length class and age of males (326–350 mm; 5 yr; Table 3). We also did not observe any males less than 298 mm, whereas the smallest female was 194 mm. The estimated age and length at which 50% of fish in our samples were males were 5.3 years and 345.5 mm (Table 2).

Few immature female (n=10) red porgies were observed in our samples. We did not find any age-1 (n=6) immature female red porgy, and most age-2 (91%, n=55) and age-3 (96%, n=99) females were sexually mature. All females age 4 or older were sexually mature. Immature females ranged in length from 194 to 302 mm and the smallest mature female was 230 mm. More than half (69%) of the fish observed were mature by the length class 226–250 mm (n=17).

Red porgy in the eastern GOM spawn from December to April. During this time period, ovaries containing either mature oocytes (spawning is imminent) or postovulatory follicles (spawning has recently occurred) were observed (Fig. 5). Throughout the rest of the year, ovaries progressed from containing only primary growth oocytes (May to August) to containing cortical alveoli and vitellogenic oocytes (September to November; Fig. 5). Ripe males were observed in every month except July and September (Fig. 6). Immature (transitional-sex-stage) males were captured throughout most of the year, but they were absent or rare just prior to and during the spawning season (November to April). For both sexes, median GSI's were low from May to October (<0.015 for females and <0.005 for males; Fig. 7). In January, median GSI's increased dramatically (0.035 for females and 0.019 for males) and then gradually decreased through August.

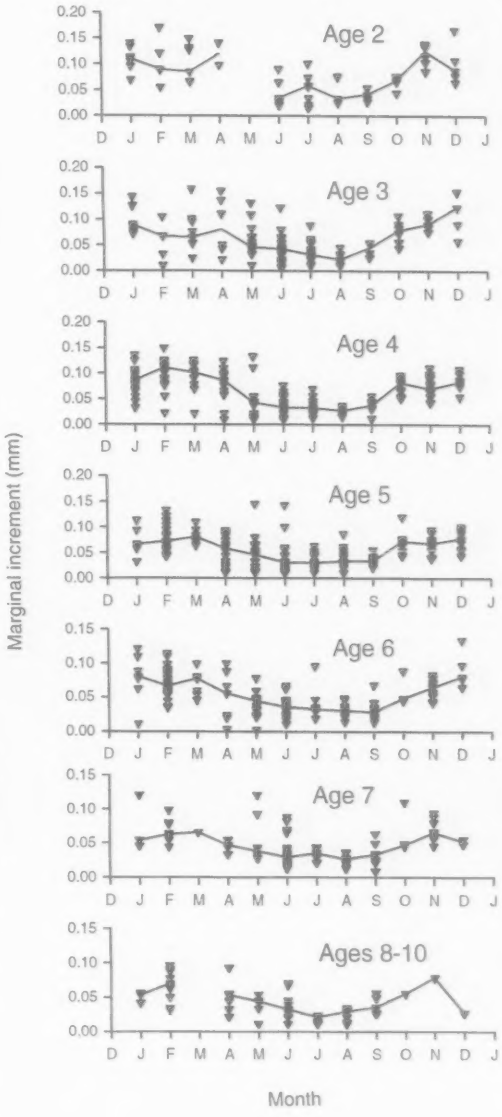

Figure 3

Marginal increments from sectioned otoliths of red porgy ages 2–10 years from the eastern Gulf of Mexico. Median monthly increments are identified by the solid line. Because of low sample sizes, ages 8–10 were pooled.

Discussion

Collections

There appeared to be a trend towards smaller red porgy in the GOM from the 1980s to the 1990s. Although landings have not increased since the early 1980s (Gulf-wide average annual landings of approximately 250,000 lbs; [Goodyear and Thompson[1]]), the length structure of the population has changed. Between 1990 and 1992, modal lengths of commercially caught fish have decreased from 357 mm to 279 mm for fish landed in Florida and from 381 mm to 254 mm for fish landed in Louisiana and Texas (Goodyear and Thompson[1]). In addition, there has been a decline from 508 mm to 381 mm in the maximum length of fish caught from headboats during 1979–91 (Goodyear and

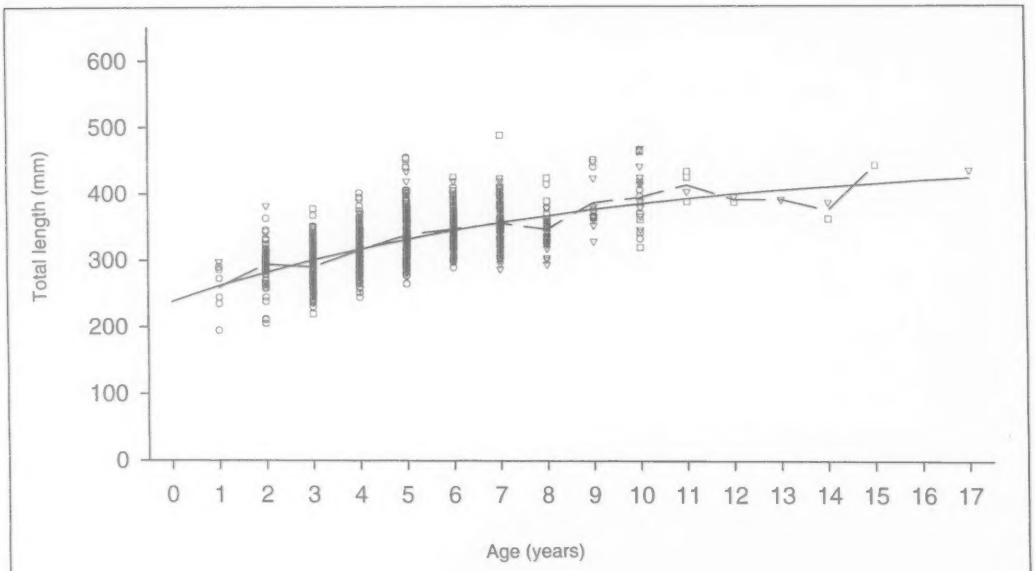

Figure 4

Total length at age, mean length at age (dashed line), and predicted length at age (solid line) of red porgy from the eastern Gulf of Mexico. Circles=females, triangles=males, and squares=unknown sex.

Thompson[1]). These trends may reflect differences between the modal length class (326–350 mm) of fish we sampled from the eastern GOM and earlier collections (349–404 mm[8]) from the Flower Garden Banks off Texas by Nelson (1988). However, because we did not obtain specific depth and gear information for fish we sampled, we cannot discount these factors to explain differences between our samples and Nelson's (1988). Decreases in average and modal lengths for red porgy in the SAB have been associated with increased fishing pressure (Collins and Sedberry, 1991; Harris and McGovern, 1997; Vaughan[5]).

Age, growth, and mortality

Although scales and otoliths have been used to determine the ages of red porgy, which structure is used, as well as how it is prepared, affects ring interpretation. Although we did not use scales to age red porgy, comparisons of ring counts determined from scales and whole otoliths from the same fish have had between 80% and 90% agreement rates (Manooch and Huntsman, 1977; Machias et al., 1998). However, Manooch and Huntsman (1977) cautioned that as age increases, both scales and whole otoliths become more difficult to interpret because the rings at the outer edge become difficult to discern. We used sectioned red porgy otoliths because most studies that have compared aging structures have found that sectioned otoliths provide more reliable estimates of age than either scales or whole otoliths, particularly for older fish (e.g. Beamish and McFarlane, 1983; Collins et al., 1987; Lowerre-Barbieri et al., 1994; Crabtree et al., 1996; Taylor et al.[9]). Sectioning otoliths also increases readability rates; Pajuelo and Lorenzo (1996) and our study were able to assign ages to 81% and 97% of the otoliths, respectively. Whole otoliths and scales used to age red porgy have provided mixed success in assigning ages to fish (54–90%: Manooch and Huntsman, 1977; Nelson, 1988; Vassilopoulou and Papaconstantinou, 1992; Harris and McGovern, 1997; Machias et al., 1998).

Opaque zones in red porgy otoliths appear to be formed annually. From marginal-increment analyses, we found that GOM red porgy form one opaque zone per year in the late spring and summer. Marginal-increment analysis has also been used by others to validate annual zone deposition in aging structures (Manooch and Huntsman, 1977; Nelson, 1988; Pajuelo and Lorenzo, 1996). Additionally, Machias et al. (1998) reported that red porgy from the Mediterranean Sea held in ponds for known periods of time formed annual rings in both scales and otoliths, and Collins et al. (1996) recaptured one oxytetracycline-injected red porgy (released in the SAB) in which the loca-

[8] Reported lengths were transformed from FL to TL by using the equation from Table 2.

[9] Taylor, R. G., J. A. Whittington, H. J. Grier, and R. E. Crabtree. In prep. Age, growth, maturation, and protandric sex reversal in the common snook, *Centropomus undecimalis*, from South Florida waters. Florida Department of Environmental Protection, 100 Eigth Avenue SE, St. Petersburg, FL 33701-5095.

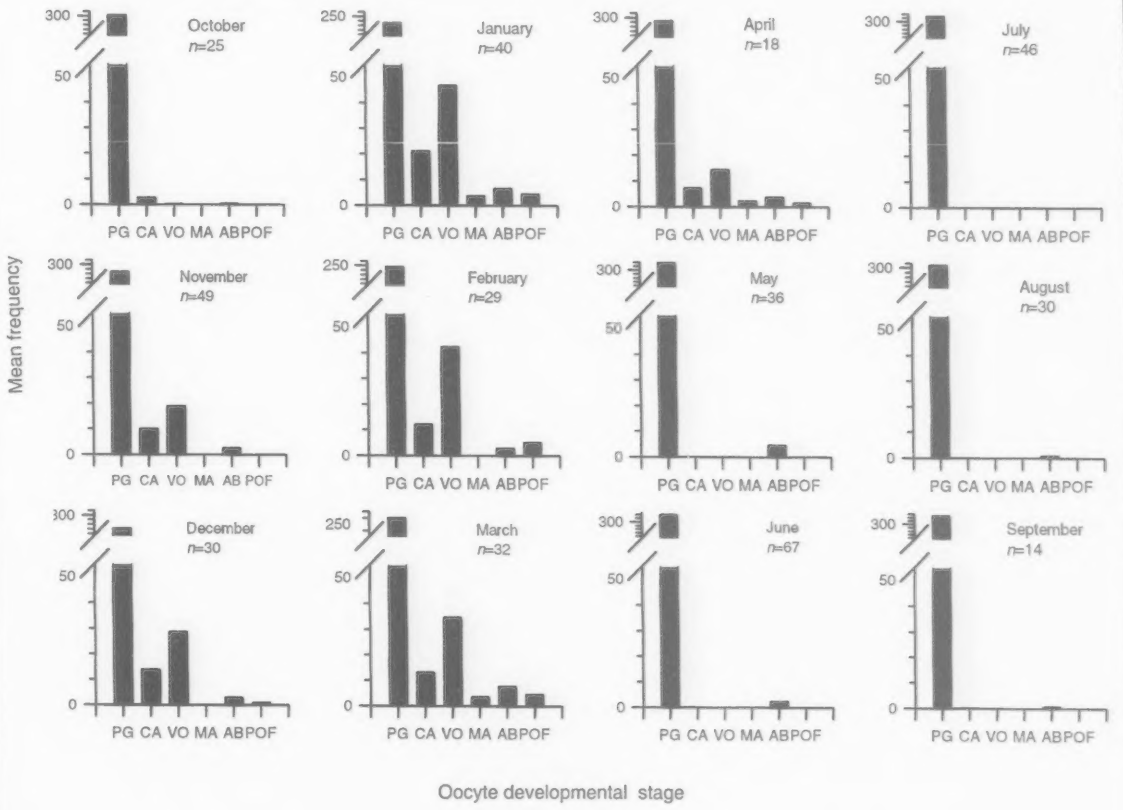

Figure 5

Average frequency of occurrence of oocyte developmental stages by month for red porgy from the eastern Gulf of Mexico. PG = primary growth oocyte, CA = cortical alveolar oocyte, VO = vitellogenic oocyte, MA = mature oocyte, AB = atretic body, and POF = postovulatory follicle.

tion of the oxytetracycline mark was consistent with the annual formation of the opaque zone.

We confirmed that red porgy are moderately long-lived fish (Manooch and Hassler, 1978). The oldest individual we aged was 17 years old, a year younger than the sectioned-otolith-based maximum age of 18 years reported for red porgy in the SAB (Vaughan[5]). Nelson (1988) reported the maximum scale-based age for this species in the GOM was 6 years and suggested that the reason for the lower maximum age than that found in the SAB (15 years by Manooch and Huntsman, 1977) was that older fish had been eliminated through higher rates of mortality. He reported that mortality rates in the western GOM (Z=0.86/yr) were much higher than those in the SAB (Z=0.44/yr; Manooch and Huntsman, 1977). However, this argument is circular because Nelson (1988) estimated mortality from catch curves that had been based on the age structure of the fish he sampled. If his age distribution was truncated owing to sampling or aging bias, then his estimates of mortality would have been higher than the true rate. Nelson's (1988) sample size was small (n=126) and geographically restricted (Flower Garden Banks off Texas) compared with the sample size of Manooch and Huntsman (1977), which was large (n=1777) and from a broad geographic region (SAB).

Our observed and predicted lengths at age were lower than those reported by Nelson (1988) for the Flower Garden off Texas. It is difficult to assess why our observed and predicted lengths at age were lower, but the limited sample size of Nelson (1988) (n=126) may not be representative of the GOM population. Other factors that may contribute to these differences include regional differences in growth within the GOM, depth of capture, hook size, or biases between the aging structures. However, Goodyear and Thompson[1] reported that the depths where red porgy were most commonly captured by GOM fisheries overlapped the depth range in which most of the fish sampled by Nelson (1988) were captured (60–90 m). Hook size

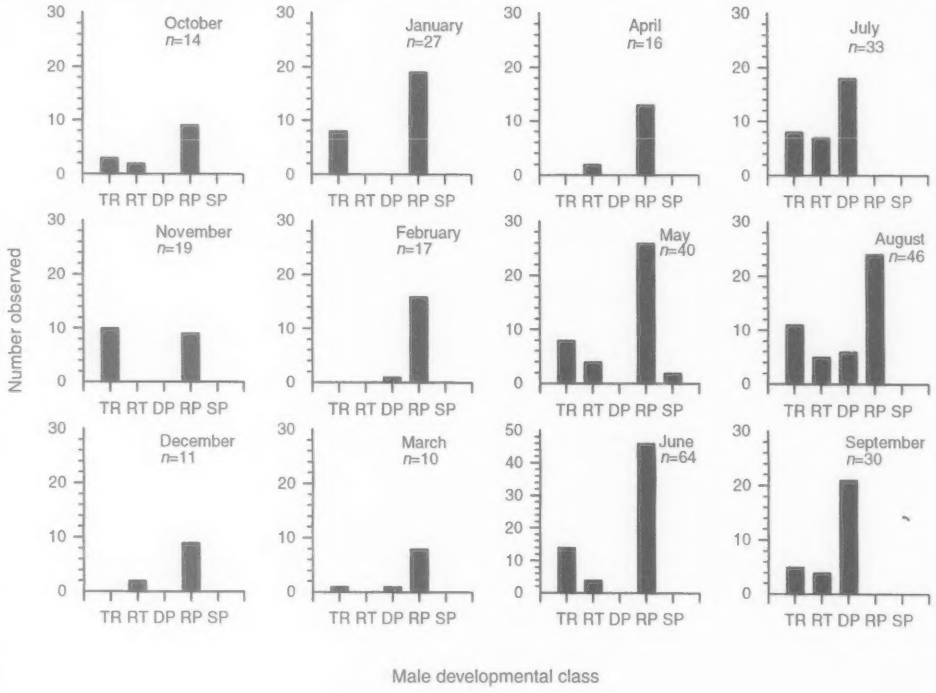

Figure 6

Frequency of occurrence of male developmental classes by month for red porgy from the eastern Gulf of Mexico. TR = transitional, RT = resting, DP = developing, RP = ripe, SP=spent

may have had a limited effect on size differences because the mean lengths at age of fish we sampled that were caught with commercial or recreational gear were not significantly different, and Nelson (1988) reported that the hook sizes did not seem to affect the size distributions of several fish species captured in his study. Finally, biases usually associated with aging structures occur at older ages when rings crowd together at the scale edge and are harder to interpret. Manooch and Huntsman (1977) were able to use scales to age red porgy to 15 years, a much greater age than the maximum age of 6 years reported by Nelson (1988). Therefore, Nelson's estimated ages may accurately describe the ages of the fish he sampled.

Changes in the average length at age between the early 1980s and present may also be the result of size-selective fishing over time, i.e. if larger fish were more vulnerable to capture, then faster-growing fish within an age class would be selectively removed from the population and the result would be a reduced mean size at age for older age classes and an underestimated L_∞ (Ricker, 1969; Pitcher and Hart, 1982). We could not demonstrate size-selective fishing pressure, but there was a shift in the size structure of red porgy stocks in the GOM towards smaller fish (Goodyear and Thompson[1])—a shift that suggests that fishing pressure is affecting the size structure of the stock. For SAB red porgy stocks, Harris and McGovern (1997) have suggested that size-selective fishing and increases in fishing mortality have caused a decrease in mean lengths at age and L_∞ in SAB red porgy stocks. The average lengths at age 6 years decreased from 451 mm in 1972–74 (Manooch and Huntsman, 1977) to 363 mm[8] in 1991–94 (Harris and McGovern, 1997), and estimated L_∞ decreased from 763 mm and 528 mm[8] for 1972–74 (Manooch and Huntsman, 1977; Harris and McGovern, 1997) to 412 mm[8] for 1991–94 (Harris and McGovern, 1997). Although differences in sampling source (fishery dependent vs. fishery independent) between Manooch and Huntsman (1977) and Harris and McGovern (1997) may have accounted for the observed differences, Harris and McGovern (1997) noted that the same changes occurred from 1979 to 1994 in their fishery-independent samples. Similar trends have been reported for vermilion snapper (*Rhomboplites aurorubens*) in the GOM (Hood and Johnson, 1999) and in the SAB (Zhao et al., 1997), which are a part of the same fishery as red porgy. However, for the SAB, Potts et al. (1998) suggested that differences in gear types may have accounted for differences in length at age reported by Zhao et al. (1997).

Red porgy were fully recruited into the GOM recreational and commercial fisheries by age 4. This is the same

age that red porgy in the Flower Garden Banks were fully recruited to the sampling gear (primarily hook-and-line) used by Nelson (1988). In the SAB, the age of full recruitment decreased from age 5 in 1972–83 to age 4 in 1984–86, probably because of higher exploitation rates (Vaughan et al., 1992). Huntsman et al. (1983) reported that the age of full recruitment to the SAB head boat fishery was 4.1–4.3 years.

Our estimates of Z (0.54–0.87/yr) are within the range of reported estimates for other populations sustaining fishing pressure. Nelson (1988) estimated Z to be 0.86/yr for fish from the Flower Garden Banks off Texas in 1980–82. In the SAB, estimates of Z increased from the early 1970s through the early 1990s: Z = 0.64/yr for SAB populations from 1972 to 1974 (Manooch and Huntsman, 1977) to Z = 1.58/yr for 1991 (Huntsman et al.[10]). Recently, Vaughan[5] estimated Z for the SAB to be between 0.90 to 0.94/yr depending on the input value of natural mortality in his stock assessment model. Vassilopoulou and Papaconstantinou (1992) reported Z = 0.34/yr for a relatively unexploited red porgy stock in the Mediterranean Sea and estimated natural mortality to be 0.28/yr.

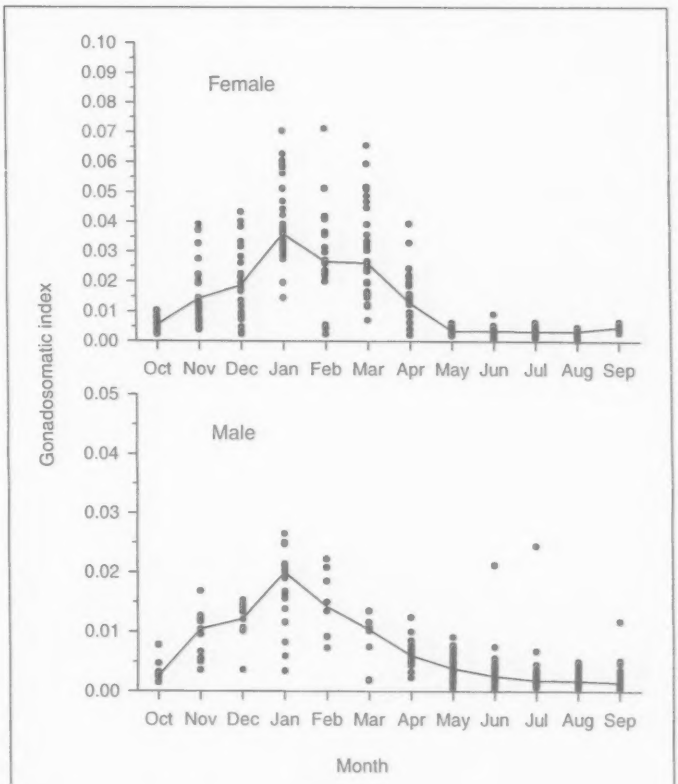

Figure 7

Monthly gonadosomatic indices (GSI) for female and male red porgy from the eastern Gulf of Mexico. Median values are connected by the solid line.

Reproduction

Protogynous hermaphrodites such as red porgy may be more susceptible to overfishing than gonochoristic species if size-selective fishing reduces the number of males available for spawning (Bannerot et al., 1987; Koenig et al., 1996). This trend is not evident for GOM red porgy. Our sex ratio of 1:1.6 had proportionally fewer females than did the 1:2.8 ratio reported by Nelson (1988) for 1980–82. In the SAB, the proportion of females has been increasing in association with fishing pressure. Manooch (1976) estimated that the sex ratio of red porgy in the SAB was 1:2.8 for 1972–74 and that proportionally more males were landed in the fishery than during later years (1:4.9–1:6.5 for 1979–1994; Harris and McGovern, 1997). The sex ratio of another GOM protogynous hermaphroditic reef-fish species, the gag (*Mycteroperca microlepis*), has been affected by overfishing (Koenig et al. 1996) in that there are proportionally fewer male gag in overfished populations than in less fished populations (male-to-female ratio of 1:76.6 for 1991–93 (Koenig et al., 1996) compared with 1:4.9 for 1977–80 [Hood and Schleider, 1992]). Koenig et al. (1996) hypothesized that because males are more aggressive in feeding, they are more likely to be captured by fishermen who target gag aggregations.

Our reported lengths at maturity (most red porgy were mature by 225 mm) were closer to lengths reported for exploited populations (<275 mm; Pajuelo and Lorenzo, 1996; Harris and McGovern, 1997) than for lightly or newly exploited populations (>276 mm; Manooch, 1976; Vassilopoulou and Papaconstantinou, 1992; Harris and McGovern, 1997). Decreases in the size at maturity for red porgy may be associated with increased fishing effort; Harris and McGovern (1997) found 27% of red porgy females were mature between 251 and 275 mm in pooled years 1979–81 compared with 54% in pooled years 1991–94.

Sexual transition occurred at smaller sizes than those reported by Nelson (1988): our estimated length at which half the population is male was 345 mm compared with 404 mm.[8] In the SAB, Harris and McGovern (1997) reported an increasing proportion of males between 351 and 400 mm over time, 12.13% in 1979–81, 32.35% in 1988–90, and 49.33% in 1991–94, which they attributed to size-selective fishing pressure. For most protogynous reef-fish

[10] Huntsman, G. R., D. S. Vaughn, and J. C. Potts. 1993. Trends in population status of the red porgy *Pagrus pagrus* in the Atlantic Ocean of North Carolina and South Carolina, USA, 1971–1992. South Atlantic Fishery Management Council, 1 South Park Circle, Charleston, SC 29422-1997.

species, the removal of males causes females to change sex (Sadovy and Shapiro, 1987). Therefore, the removal of larger fish (males) by fisheries causes smaller and smaller females to change sex and results in an increase in the proportion of smaller-size males.

Based on monthly changes in the percentage of fish in the various maturity classes, the frequencies of different oocyte stages, and GSI, we believe that red porgy spawn in the GOM from January to April. Our findings are consistent with spawning season observations reported for red porgy in the GOM by Nelson (1988), in the SAB by Manooch (1976), in the Canary Islands by Pajuelo and Lorenzo (1996), and in the Mediterranean Sea by Vassilopoulou (1989) and Vassilopoulou and Papaconstantinou (1992).

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Abstract—Aerial surveys to estimate the numbers of beluga whales, *Delphinapterus leucas*, were flown in James Bay, eastern Hudson Bay, and Ungava Bay in Canada in the summer of 1993 on transects systematically spaced 5 or 10 nmi apart. In James Bay and eastern Hudson Bay line-transect methods were used. In Ungava Bay strip transects were used, and off-transect sightings were also recorded. Beluga whales were also counted on coastal flights in eastern Hudson Bay and Ungava Bay. James Bay and eastern Hudson Bay were surveyed in August; Ungava Bay in July and again in August. Watches were kept from land at estuaries in eastern Hudson Bay in 1993 and in Ungava Bay in 1992 and 1993.

The estimates of detectable beluga whales (uncorrected for diving and observer errors) were 3141 (SE=787) in James Bay and 1014 (SE=421) in eastern Hudson Bay. A further 115–148 beluga whales were seen near the coast of eastern Hudson Bay during the coastal survey, but mostly away from traditionally used estuaries. The estimate for James Bay was nearly three times the previous estimate, made in 1985, possibly because ice cover in James Bay was much lower in 1993 than in the 1985 survey. The 1993 estimate for eastern Hudson Bay was close to that for 1985. No beluga whales were seen during aerial transects in Ungava Bay, but they were seen off-transect and on coastal flights, mostly in or near the Whale River estuary in southern Ungava Bay. The largest group sighted and the greatest number seen in any day consisted of 20 individuals, a minimum size for the summer population in Ungava Bay. An upper 90% confidence limit for summer numbers is imprecisely estimated at 150.

Neither the coastal surveys nor the land-based observations in Hudson Bay and Ungava Bay indicated the presence of large, dense herds that might have been inefficiently sampled by transect survey.

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Numbers and distribution of beluga whales, *Delphinapterus leucas*, in James Bay, eastern Hudson Bay, and Ungava Bay in Canada during the summer of 1993

Michael C. S. Kingsley

Canadian Department of Fisheries and Oceans
Maurice Lamontagne Institute
850, Route de la mer
Mont-Joli, P.Q. G5H 3Z4
Present address: Pinngortitaleriffik—Greenland Institute of Natural Resources
P.O. Box 570
DK-3900 Nuuk
Greenland
E-mail address:mcsk@natur.gl

James, Hudson and Ungava bays are summering areas for stocks of beluga whales (*Delphinapterus leucas*) (Sergeant and Brodie, 1975; Finley et al., 1982; Smith and Hammill, 1986; Richard et al., 1990). There are several apparently separate summer groups, which include a summer group of ~23,000 individuals in western Hudson Bay, a group of 1500 individuals in the eastern Hudson Bay arc, and a few individuals in Ungava Bay (Smith and Hammill, 1986; Richard et al., 1990). Beluga whales, probably composing other separate groups, also summer in southern Hudson Bay (Richard, 1993) and James Bay (Smith and Hammill, 1986).

A land claim agreement was signed between the Inuit of the central and eastern Canadian Arctic and the Government of Canada in 1990 (Anonymous, 1993). In eastern Hudson Bay, this land agreement defined a marine area around the Belcher Islands (the "Nunavut Settlement Area") for the use of the beneficiaries of that agreement (Figs. 1 and 2). It also defined an area north and east of the settlement area (the "Equal Use and Occupancy Area") to be shared by the Inuit of Nunavut and those of northern Quebec. Other provisions of the agreement, and of the earlier James Bay and Northern Quebec Agreement, assured the aboriginal people of a right to hunt beluga whales in these waters.

The hunting of beluga whales is valued by Inuit in northern Canada as a means of procuring food, as a tradition helping to define their culture, and as a recreation. Maintaining beluga whale hunting, and stocks adequate to support it, are important objectives for the Inuits. Commercial hunting in the 19th century severely reduced numbers of beluga whales on the eastern coast of Hudson Bay and in Ungava Bay and they have not yet recovered (Reeves and Mitchell, 1987a; 1987b; 1989). These stocks were listed as "threatened" and "endangered," respectively, by the Committee on the Status of Endangered Wildlife in Canada (Campbell, 1993), and exploitation still occurs (DFO, 1996; NAMMCO, 1999) A low reproductive rate limits the species's potential for increase (Sergeant, 1981; Kingsley, 1989); therefore careful monitoring and management of stocks are appropriate.

Population management requires periodic evaluations of stock size, as a basis for setting harvest levels and for estimating the effect of harvest on the population trend. Beluga whale stocks are evaluated by aerial survey in their summering areas. The previous, and first, offshore aerial survey of James Bay, eastern Hudson Bay, and Ungava Bay was flown in summer 1985 (Smith and Hammill, 1986), and the development in the early 1990s of a beluga whale management plan for northern Quebec rendered it timely to update information on the population.

This article reports the results of aerial surveys flown in summer 1993. A

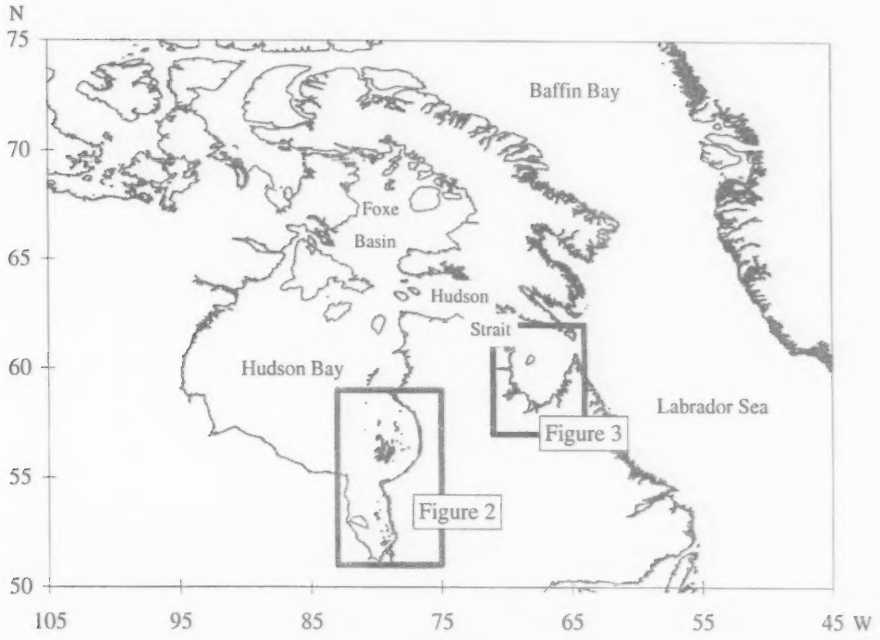

Figure 1

Map of northeastern Canada, showing the locations of the 1993 beluga whale aerial surveys in James Bay, eastern Hudson Bay, and Ungava Bay.

systematic transect survey was flown over offshore areas of James Bay, eastern Hudson Bay, and Ungava Bay (Figs. 1–3). However, summering beluga whales often form dense coastal concentrations, which are inefficiently estimated by sample survey. Therefore, coastal surveys were also flown in eastern Hudson Bay and Ungava Bay to check whether large numbers in concentration areas might have caused serious errors in the results of sample surveys. To the same end, watches were kept over known estuarine concentration areas from vantage points on land in 1992 and 1993.

Methods

Beluga whales concentrate in and around the mouths of rivers in summer, and this habit largely defines accepted stocks (Brown Gladden et al., 1997). Therefore aerial surveys for stock assessment are normally carried out in summer in these areas. The survey area for this study comprised James Bay, the eastern Hudson Bay arc north to 59°N and as far west as 80°20′W, and Ungava Bay. This area was similar to that covered by the previous aerial survey of these stocks in 1985 (Smith and Hammill, 1986). Beluga whales are uncommon in summer along the northern part of the eastern coast of Hudson Bay and the southern coast of Hudson Strait (Finley et al., 1982; Smith and Hammill, 1986); therefore the survey did not include these areas.

The transects in James Bay and eastern Hudson Bay were systematically spaced east–west lines similar to those used in 1985 (Smith and Hammill, 1986) (Fig. 2). They were on exact 10′ lines of latitude (i.e. 18.52 km apart) from the southern end of James Bay at 51°10′N as far as 58°50′N near Inukjuak, and additional lines were interpolated at 5′ (9.26-km) intervals between 55°35′N and 57°35′N, i.e. in the central part of the Hudson Bay arc.

The survey of Ungava Bay was also based on systematic designs (Fig. 3). South of 59°30′N, the initial design had north–south transects on every 15th minute of longitude, a spacing approximately equal to 7.5 minutes of latitude (13.9 km). North of this line the transects lay east–west on every tenth minute of latitude, i.e. 18.52 km apart.

Earlier surveys of Ungava Bay had detected few beluga whales (Finley, 1982; Smith and Hammill, 1986). Inuk hunters had suggested that flying at different times in the summer might produce different results; therefore the Ungava Bay survey was flown twice: in mid-July and in late August. In both surveys, sections of the coastline were followed and surveyed when ferrying to and from transect blocks, so that the coastline, particularly near the logistic base at Kuujjuak, was repeatedly covered.

The transect survey of James Bay and eastern Hudson Bay was flown in a Cessna 337 aircraft, at 1500 feet (457 m) above sea level at about 130 knots, (67 m/s), and navigated by GPS. The aircraft was equipped with flat windows. Observers sat in the two seats behind the pilot. Line-transect survey methods were used, in which all sightings were recorded with their distance from the transect line, and a sighting curve was subsequently calculated to correct for the decreasing detectability of targets with distance.

The angle of view from the horizontal was measured with Suunto inclinometers. Records were made with time-coding tape recorders and were transcribed daily. Ground speeds were calculated from the elapsed time on the transect and sighting positions were interpolated along transects. The state of the sea was assessed and recorded by using the Beaufort Scale of wind force; survey plans included not flying in conditions over Beaufort 4 (i.e. over 10 knots or 5.14 m/s).

The coastline of the eastern Hudson Bay arc was surveyed once, on 21 August, in a flat-windowed "Twin Otter" aircraft flying at 500–1000 ft (152–305 m). The observers, two to seven in number depending on the survey segment, were members of local hunters' and trappers' associations; they sat behind the pilots and recorded observations directly onto sighting maps. The flight line from Kuujjuaraapik followed the mainland coastline northbound to Inukjuak. The southbound leg was flown on the offshore side of the chains of islands close to the coast, and the plane made a detour to survey Richmond Gulf. It flew as far south as the Vauquelin River before returning to end at Kuujjuaraapik (Fig. 2).

The Ungava Bay surveys used strip-transect methods. A "Twin Otter" aircraft was flown at an altitude of 1500 feet (457 m). The transect survey used a systematic design with a strip width of 600 m on each side of the aircraft, but sightings were so few that all were recorded, on- or off-effort and on- or off-transect. Ferry flights to the start of and from the end of each day's transect pattern followed the coastline, detouring to search the largest bays and estuaries. The entire coast was covered in this way, some stretches several times.

Observations made from land at estuaries frequented by beluga whales in summer were a supplementary source of information from which it was possible to assess the probability that large estuarine concentrations had been inefficiently estimated by transect sample survey. Local observers manned camps at the Little Whale River and at the Nastapoca River in eastern Hudson Bay in 1993,[1] and in southern Ungava Bay in 1992[2] and 1993[3] (Fig. 3). From vantage points, the estuary areas were scanned regularly for beluga whales. The estuaries of the Little Whale and Nastapoca rivers are less than 1 km long, and easily covered, but the Whale River estuary in southern Ungava Bay could not be completely covered. The objective was to scan five times a day, at three-hour intervals; but weather sometimes interfered with this schedule. Not only numbers, age class, and behavior of beluga whales were noted, but also boat and air traffic, visibility, wind, weather, and tide.

Line-transect methods were used to analyze the data from James and Hudson Bays. Such methods involved fitting to the sighting data a sighting probability curve $g(x)$, i.e. the probability that an animal group at distance x from the

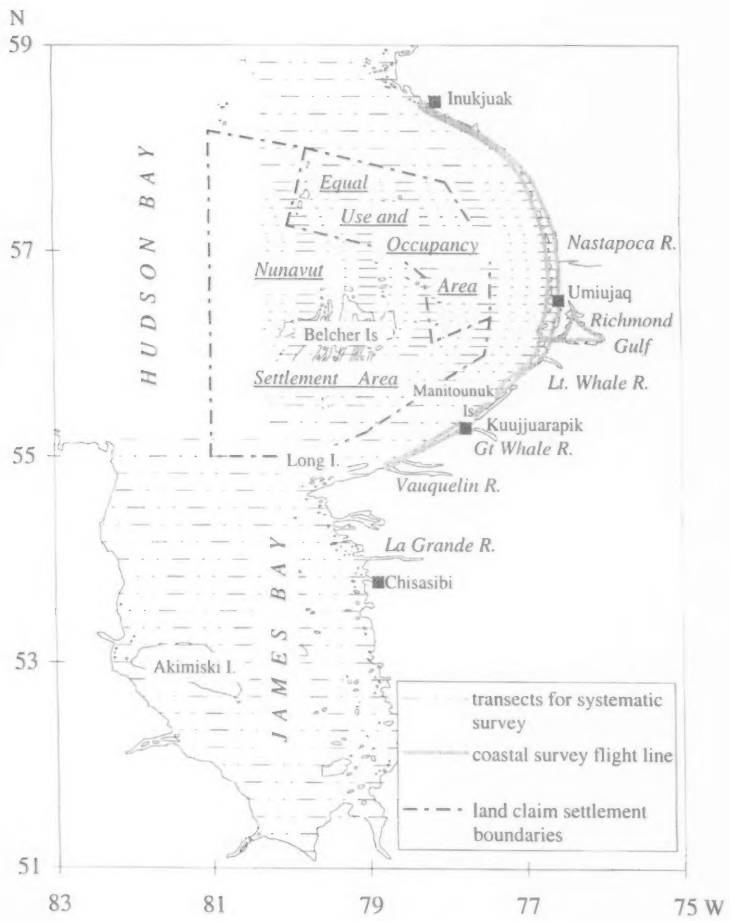

Figure 2

Systematic design for aerial transect survey of beluga whales in James Bay and eastern Hudson Bay, August 1993.

[1] Doidge, D. W. 1994. Land-based observation of beluga whales at the Little Whale and Nastapoka rivers, eastern Hudson Bay, summer 1993. Report prepared by Makivik Corp., C.P. 179, Kuujjuaq, P.Q. J0M 1C0 Canada, 30 p.

[2] Makivik Corp. 1993. Land-based observations of belugas in Ungava Bay, summer 1992. Report prepared by Makivik Corp., C.P. 179, Kuujjuaq, P.Q. J0M 1C0 Canada. 7 p.

[3] Doidge, D.W., and A. H. Gordon. 1994. Land-based observations of beluga at Tuututuup Nuvunga, southern Ungava Bay, summer 1993. Report prepared by Makivik Corp., C.P. 179, Kuujjuaq, P.Q. J0M 1C0 Canada, 13 p.

track-line is detected. Commonly, line-transect analysis assumes that 1) $g(0)$ is unity and 2) $g(x)$ is never increasing with x. An associated shape criterion, which improves the behavior of estimates obtained by line-transect survey (Burnham et al., 1980; Buckland, 1985), suggests that the sighting curve should have a "shoulder" or plateau at small x.

Richards' (1959) sigmoidal growth curve, reversed left-to-right, was chosen for its flexibility to fit $g(x)$. The ordinate at the point of inflection was constrained to be less than 0.9. Because of difficulty in seeing straight down from a flat-windowed aircraft, no animals could be seen close to the transect line; therefore, close to the transect line, an increase in $g(x)$ was modeled by an increasing sine^2 function (Fig. 4). It was assumed that $g_{max} = 1$, i.e. that all surface-visible beluga whales situated at the best distance would be detected. Detection bias would occur if this assumption was incorrect.

The data were truncated at 6000 ft (1829 m) from the trackline; beyond this distance, sightings were few, and measured sighting angles and counts of numbers were imprecise. Within this range, the sighting curve was fitted by maximum likelihood to the distribution of distances from the trackline to individual beluga whales, not to the distribution of sighted groups (Hiby and Hammond, 1989). A single sighting curve was fitted, and a single estimate of k was calculated, and for the survey of James Bay and eastern Hudson Bay, all three strata were pooled. It was integrated numerically to calculate the effective strip width.

The transect counts were expanded to an estimate of detectable numbers:

$$\hat{N} = \sum_{s=1}^{S} \hat{N}_s = \sum_{s=1}^{S} kT_s B_s, \qquad [1]$$

where T_s = the transect spacing (km);
B_s = the total count of beluga whales in the s^{th} stratum; and
k = the survey expansion factor (/km) i.e. the reciprocal of the two-sided effective strip width.

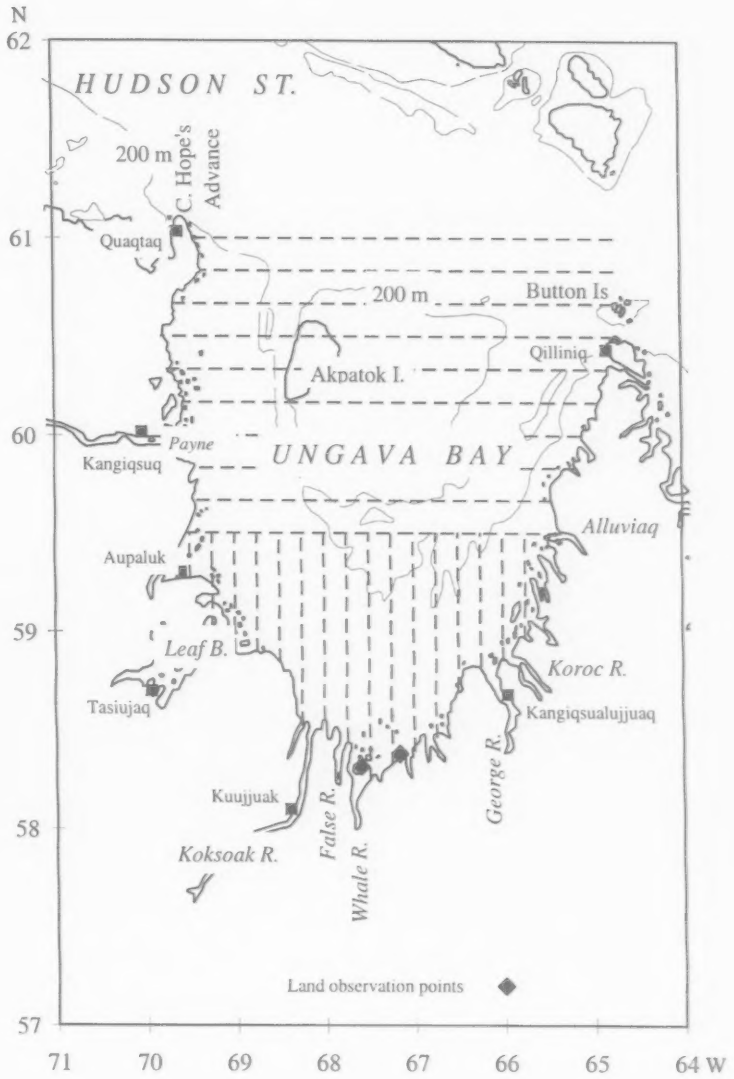

Figure 3

Map of Ungava Bay with the survey design for aerial surveys in July and August 1993.

The uncertainty of N_s was estimated as the sum of V_{s1}, the component from sampling the spatial distribution of beluga whales in the stratum; and V_{s2}, that was due to uncertainty in the estimation of k. V_{s1} was estimated by a serial difference method appropriate to systematic sampling (Cochran, 1977):

$$V_{s1} = kT_s \cdot (kT_s - 1) \cdot \frac{J_s}{J_s - 1} \cdot \frac{\sum_{j=1}^{J_s - 1} (B_j - B_{j+1})^2}{2}, \qquad [2]$$

where B_j beluga whales were sighted on the j^{th} of J_s transects in stratum s.

V_{s2}, the component of sampling error due to uncertainty in the estimation of the effective strip width, was estimated by

$$V_{s2} = \text{var}(k) \cdot (T_s \cdot B_s)^2. \quad [3]$$

The sighting curve was fitted to nonindependent individuals instead of to independently sighted groups, so the standard error of k was estimated by resampling (Hiby and Hammond, 1989). The standard jack-knife method was used (Efron and Tibshirani, 1993), and sightings, presumed independent, were taken as observational units. Maximum-likelihood estimates are not necessarily unbiased in small samples but may be subject to sample-size bias. The effective number of sightings,[4] 57.7, was less than the recommended minimum (Buckland et al., 1993); therefore sample-size bias in the estimate of the survey expansion factor was reduced by using the standard jack-knife bias reduction (Efron and Tibshirani, 1993; Buckland et al., 1993; Kingsley and Reeves, 1998).

Sightings made on stratum-boundary transects where transect spacing changed were given half weight in each stratum.

Few sightings were made on the transect sample survey in Ungava Bay, and none within the designed survey strip. The sightings made outside the transect strip were converted to a population estimate by assuming an effective strip width based on statistics from other line-transect surveys that had used similar platforms. No standard error was calculated, but an upper confidence limit on the number of groups was calculated by assuming independent binomial sighting probabilities and by answering the question "Given that the sampling fraction was f, how many groups could there be for the chance of seeing none or one to be less than p%?"

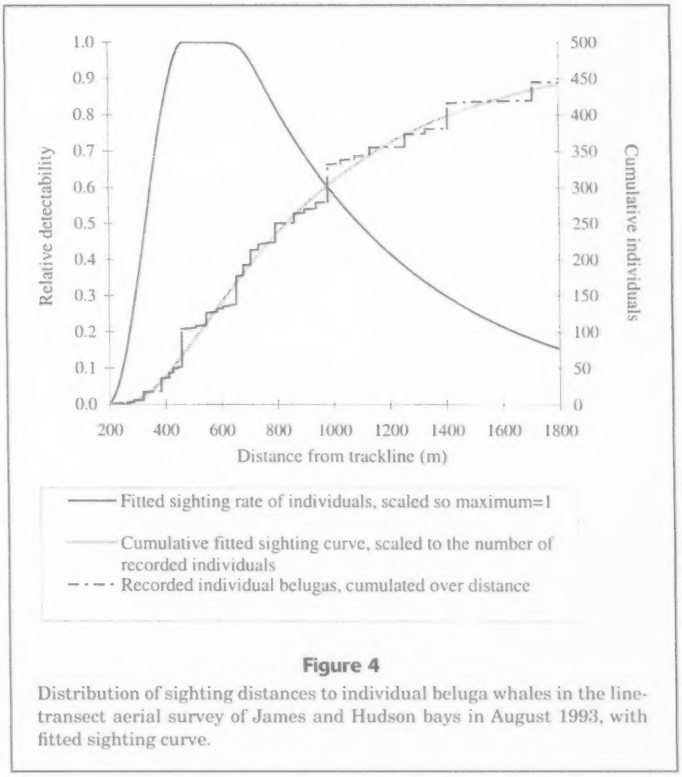

Figure 4

Distribution of sighting distances to individual beluga whales in the line-transect aerial survey of James and Hudson bays in August 1993, with fitted sighting curve.

Results

The survey in James Bay was flown quickly in good conditions from 12 August through 14 August. Winds were light and, apart from occasional fog patches, survey conditions were good. The southern part of eastern Hudson Bay was flown on 15–17 August with light winds and good visibility. Aircraft problems imposed a delay from 18 through 20 August, and on 21 and 24 August there were strong winds. Richmond Gulf was surveyed on 16 August (Fig. 2).

The field of view was limited by the flat windows of the aircraft. No observations were recorded closer than a viewing angle of 65° from the horizontal (at a flying height of 1500 feet, 213 m from the line), and few closer than 55° (320 m) (Fig. 4). Sighting distances were grouped, because the observers tended to round sighting angles. The last-digit frequencies of the recorded angles were analyzed, and it was found that rounding to the nearest 5° was mostly at the expense of the adjacent marks, i.e. those with a remainder of 1° or 4°. Against an expectation of equal frequency of last digits, rounding caused a mean absolute error of 0.42° and was not expected to bias results or to increase uncertainties. Recorded mean group size increased slightly with sighting distance.

The sighting frequency reached its maximum at 467 m (44.2°) and dropped off sharply beyond about 670 m (35°) (Fig. 4). There were few sightings of beluga whales in Hudson Bay; therefore one sighting curve was fitted to the data for all strata. The bias-reduced survey expansion factor was 0.575/km (SE=0.074).

Beluga whales were widely distributed in James Bay (Fig. 5A). There were 123 sightings in 4520 km of transect (27/1000 km), comprising 295 individuals (65/1000 km) (Table 1). Line-transect analysis gave an estimate of 3141 detectable beluga whales for James Bay (Table 2). This number is about three times the estimate obtained by Smith and Hammill (1986). However, their survey was earlier, when a lot of ice still remained in northwest James Bay and may have affected the distribution of these whales. The highest densities in the present survey were in this area. In eastern Hudson Bay (Fig. 5B) there were 63 sightings on 7100 km of transect (9/1000 km) comprising 150 beluga whales (21/1000 km) (Table 2).

[4] Effective number of sightings is defined here as the number of animals seen divided by the contraharmonic mean of group size.

Table 1

Sizes of beluga whale groups sighted on transect survey flights in James Bay, eastern Hudson Bay, and Ungava Bay, during the summer of 1993. CHM = contraharmonic mean, i.e. the size of the group containing the average beluga.

	Sightings	No. of beluga whales	Group size			Effective no. of sightings
			Mean	CHM	SD	
James Bay	123	295	2.40	6.29	3.05	46.9
Hudson Bay	63	150	2.34	10.52	4.40	14.2
Ungava Bay (July survey)	1[1]	4	5.6[2]	13.5[2]	6.93[2]	
Ungava Bay (August survey)	1[1]	19				

[1] These transect-survey sightings were outside the designed survey strip. No sightings were made within the strip.
[2] These statistics are for all 12 sightings in Ungava Bay, including coastal reconnaissance flights, and for both surveys.

Error coefficients of variation (ECV) ranged from 25% for James Bay to 86% for the northern stratum of widely spaced transects in eastern Hudson Bay, where the estimate was based on 10.5 sightings made on 2.5 transects (Table 3). The ECV of the overall estimate was 23%. The use of a common sighting curve reduced the estimated standard errors for individual strata. Uncertainty in k composed only 2% and 20% of the error variances for the two Hudson Bay strata, but 32% of the overall error variance.

On the coastal survey of eastern Hudson Bay, 13 groups of beluga whales were seen, distributed from the northern end of the offshore chain of islands to south of the Great Whale River (Fig. 6). The total number of individuals was 115–148. One large group—70 to 100 individuals—was seen, close to the Manitounuk Islands.[5] A few beluga whales were seen in the Great Whale and Little Whale rivers.

Observers on land at the Little Whale River saw beluga whales on 14 of the 22 observation days. The mean daily maximum count for days on which the whales were seen was 40.4 individuals (range 5–130). At the Nastapoca River, beluga whales were present on 7 of 13 observation days, and the mean daily maximum was 23.3 (1–53). Even on days when they were seen, beluga whales were not continuously present: at the Little Whale River; none were seen on 45% of scans made on days when they were seen at least once, and at the Nastapoca, River, 54% of scans on such days showed no sightings.

The first aerial survey in Ungava Bay was flown on 15–19 July, 1993. It was limited by dense pack ice that remained in the central and northern part of the bay, heavy enough

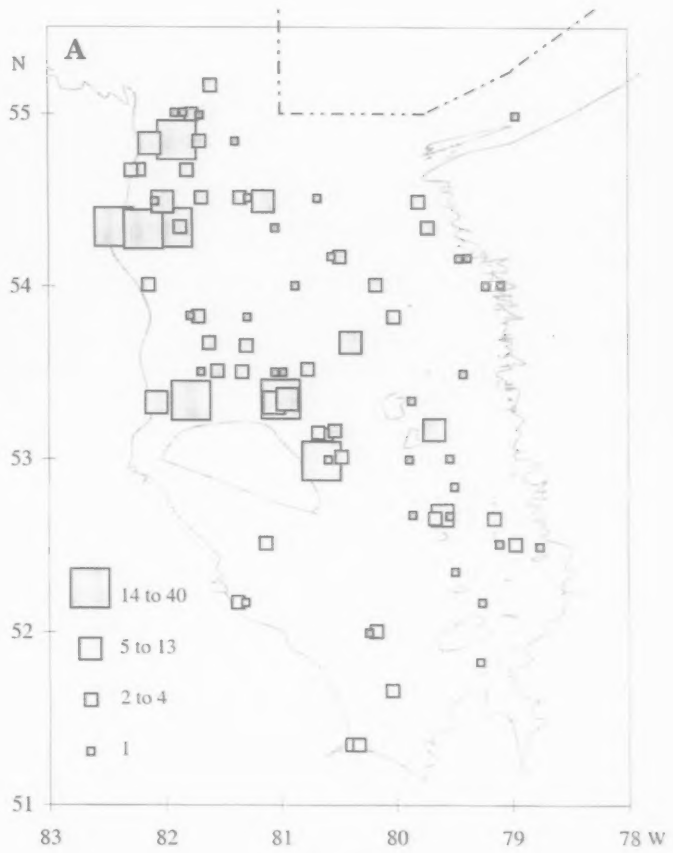

Figure 5

Beluga whale sightings on line-transect aerial survey of (**A**) James Bay and (**B**) eastern Hudson Bay, in August 1993

[5] Doidge, D. W. 1993. Coastal reconnaissance survey for belugas in eastern Hudson Bay, August 21, 1993. Report prepared for the Department of Fisheries and Oceans, 104, rue Dalhousie, Quebec P.Q. G1K 4B8, Canada by Makivik Corp., C.P. 179, Kuujjuaq, P.Q. J0M 1C0 Canada, 8 p.

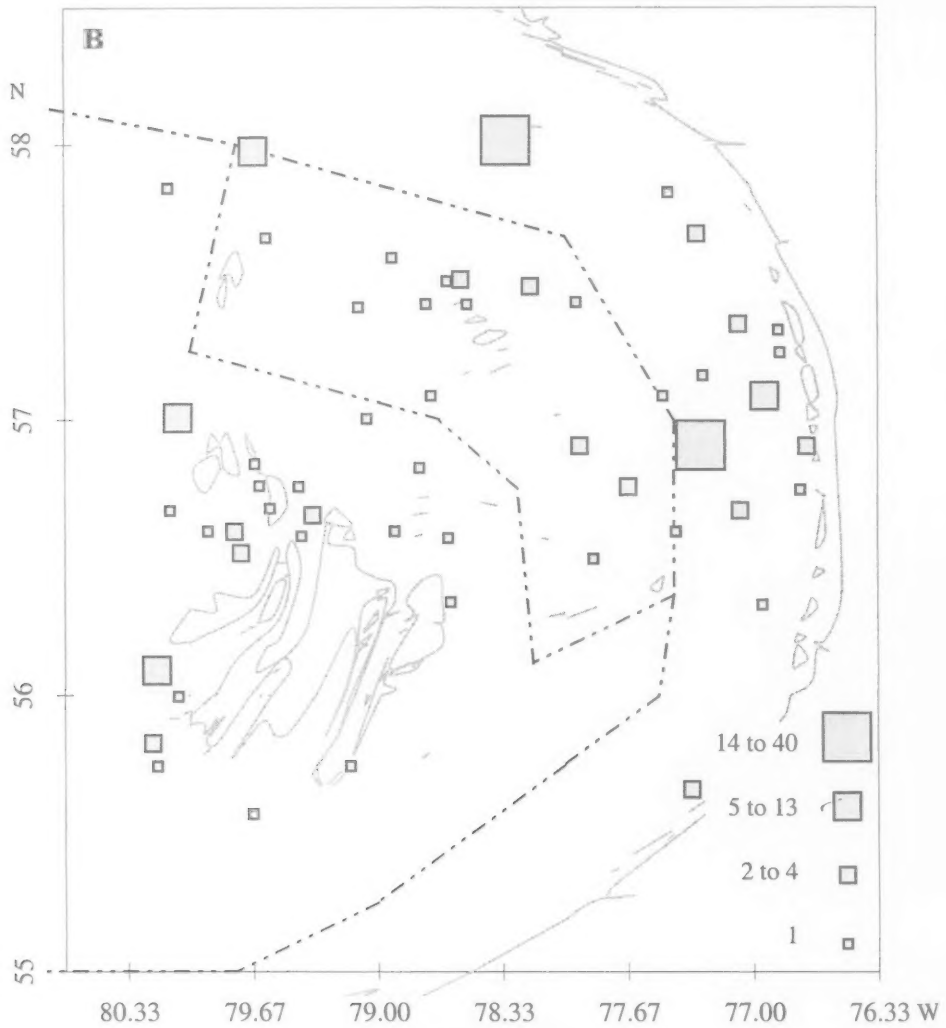

Figure 5 (continued)

to restrict the distribution of beluga whales and to make it difficult to count them. The survey was not extended into this area of heavy ice. North–south transects were flown in southern Ungava Bay, south of the ice. The second survey, 24–29 August, was flown over open water throughout Ungava Bay. However, some planned flight patterns were limited by fog in northeastern Ungava Bay.

In Ungava Bay, beluga whales were seen on four of five flying days in July, with a maximum daily count of 20 individuals in one sighting, and on three of six flying days in August, with 20 individuals in two sightings on the best day (Table 3). In the two surveys together, beluga whales were sighted in the Whale River estuary on six of seven overflights. There were also two sightings in southern Ungava Bay close to the Whale River, and two sightings of small groups in western Ungava Bay. The mean sighting size was 5.6 groups (SE=2.0).

However, no beluga whales were seen within the designed survey strip. From independent binomial sighting probabilities, corresponding upper 90% CLs would be 25.5 groups for the first survey and 34.3 groups for the second (assuming the mean group size of 5.6, equal to 143 and 192 animals). One off-strip sighting was made on a sample survey flight during each survey, but no distance measurements were made. Off-strip effort is considered to have an outer visibility limit similar to that estimated by line transect analysis of the data for James Bay and eastern Hudson Bay, but an inner limiting angle similar to the 72° estimated for a similar platform by Harwood et al. (1996). This would result in a strip width of about

Table 2

Estimates of numbers of beluga whales by stratum and overall, in James Bay, eastern Hudson Bay, and Ungava Bay, during August 1993.

Stratum	Count of beluga	No. of transects	Transect spacing (km)	N_{est}[1]	V_1[2] (10^3)	V_2[3] (10^3)	SE
James Bay (including southern Hudson Bay arc)	295	26.5	18.52	3141	454	165	787
Central Hudson Bay arc: closely spaced transects	109.5	26	9.26	583	25	6	174
Northern Hudson Bay arc: widely spaced transects	40.5	7.5	18.52	431	135	3	372
Central and northern Hudson Bay total	150	33.5	—	1014	160	17	421
Ungava Bay (July survey)	4[4]	15	13.9	38[5]	—	—	—
Ungava Bay (August survey)	19[4]	16	18.52	50[5]	—	—	—

[1] The survey expansion factor k for the line-transect survey in James Bay and eastern Hudson Bay, including the jack-knife bias correction, was 0.575/km with a jack-knife-estimated SE of 0.0742/km. The one-side effective strip width was 870 m.

[2] V_1 is the component of error variance due to the variability in the encounter rate and consequent uncertainty in estimating its mean.

[3] V_2 is the component of error variance due to the uncertainty in estimating the effective strip width.

[4] These sightings were made outside the designed transect strip of the strip-transect survey, and estimates are based on an assumed effective strip width of 1020 m each side; k = 0.49/km (see text).

[5] Population estimates are based on the mean size (5.6) of all groups sighted on reconnaissance and transect flights.

Table 3

Sightings of beluga whales in aerial surveys of Ungava Bay during July and August 1993.

Date	Area covered by flight	No. seen	Where seen	When seen
15 Jul	Transects in southeast Ungava Bay; and the southeast coast from the Kosoak River to the Koroc River			
16 Jul	Transects in southwest Ungava Bay; and the southwest coast from the Whale River to the Leaf River	3 adult	Whale River estuary	between transects
17 Jul	The southern and eastern coasts from the Koksoak River to the Button Islands	20 mixed	Whale River estuary	on coastal flight
18 Jul	The western coast from the Koksoak River to Quaqtaq	2 adult + possibly 1 calf 1 adult	NW Ungava Bay near Leaf Bay	
19 Jul	Transects in southern Ungava Bay between the Leaf River and the George River; also the south coast from the George River to False River	2 adult + cow-calf pair 1 adult; 1 adult + 1 juv. + 1 neonate; 1 adult	SE Ungava Bay Whale River estuary Whale River estuary Whale River estuary	on transect[1] on coastal flight on coastal flight on coastal flight
24 Aug	The western coast, from the Koksoak River to Quaqtaq	10	Whale River mouth	on coastal flight
25 Aug	The southern coast, from the Whale River to the George River	2	Whale River mouth	on coastal flight
26 Aug	Transects in southwest Ungava Bay, and the coasts of Leaf Bay and the Leaf River			
27 Aug	Transects in southeast Ungava Bay, and the southeast coast from Whale River to Alluviaq	19 1	15 km E of Whale River 10 km E of Whale River	on transect[1] on coastal flight
28 Aug	Transects in northwest Ungava Bay, and the coast of Akpatok Island			
29 Aug	Transects in northeast Ungava Bay, and the northeast coast from Alluviaq to the Button Islands			

[1] Sightings made "on transect" were outside the designed transect strip of 600 m each side of the aircraft.

1020 m on each side and survey expansion factors of 6.8 for the first survey and 9 for the second. Resulting estimates would be 6.8 and 9 groups (38 and 50 whales), with approximate 90% upper CLs of 25.0 and 33.8 (119 and 157 whales, if mean group size was 5.6). These estimates and confidence limits were imprecise and did not account for the uncertainty of mean group size or for the known lower bound on numbers.

The large tidal range in southern Ungava Bay creates extensive foreshore flats, and few beluga whales were sighted from the observation points on land. In 1992, 160 scans made over 35 days between 5 Aug. and 30 Sept. showed a total of 24 individuals. In 1993, 145 scans over 29 days in June and July resulted in four sightings totaling 8 individuals; 68 scans over 15 days in August and September resulted in three observations totaling 30 individuals. The largest count in any sighting was 17.

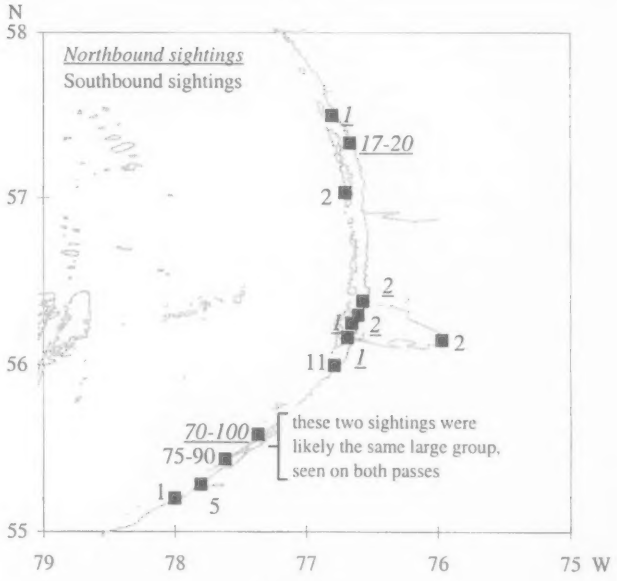

Figure 6

Sightings of beluga whales on coastal aerial survey of eastern Hudson Bay, 21 August 1993.

Discussion

The 1993 estimate of surface-visible beluga whales in James Bay, about 3140, was 2.6 times that of the previous survey (Smith and Hammill, 1986). In that survey, flown in early August, ice cover was still present in northwestern James Bay; most groups were composed of fewer than 5 animals and they were distributed in the southern part of James Bay (Smith and Hammill, 1986, Fig. 1). In the present survey, there was no ice and there were many observations of larger groups. The highest densities were north of Akimiski Island and up the western side of James Bay, where many groups were found in shallow turbid water close to shore (Fig. 5A). The beluga whales may have been distributed differently in the two surveys because of the ice that still remained at survey time in 1985.

It is difficult to ascertain the origin of this population. Significant numbers of beluga whales were once reported wintering in James Bay (Jonkel, 1969) prompting the suggestion that a large part of that population might be resident (Sergeant, 1986). However, a resident population could not increase fast enough to account for the difference between the 1985 estimate and the present one (Eberhardt and Siniff, 1977; Sergeant, 1981; Kingsley, 1989; Doidge, 1990). In 1985 there was significant ice cover in northwest James Bay, and beluga whales moving into James Bay from southwestern Hudson Bay may have been delayed by the ice in 1985, and not in 1993. However, Richard (1993) suggested that the principal southward spring migration route for James Bay beluga whales may be down the east coast of Hudson Bay, in which case ice in northwest James Bay would not have been a barrier. Alternatively, the populations in western and southwestern Hudson Bay (Richard et al., 1990; Richard, 1993) may have been colonizing James Bay. A small fraction of the estimated 23,000 beluga whales of the western Hudson Bay stock would have had a large effect on survey counts if they had been present in James Bay.

The estimated density of beluga whales in eastern Hudson Bay was slightly greater than the 1985 transect-survey estimate (Smith and Hammill, 1986 Table 1). However, for the latter survey, strip transects (with a total width of 2000 m) were used. This distance probably exceeds the range at which beluga whales can be effectively counted in a survey in the Beaufort Sea. With the same platform, target species, and type of aircraft window, Harwood et al. (1996) estimated an effective strip width of about 1300 m. The 1985 strip-transect estimate may have been biased downward in relation to the present survey. In 1985, 200 beluga whales were counted; in 1993, 150 whales were counted on the same transects.

Few beluga whales were seen on the coastal survey of eastern Hudson Bay in 1993. There were no large concentrations in the mouths of rivers, but scattered small groups and probably only one large group. The total was less than 150 individuals. The land-based observations in 1993 also did not record large groups in the estuaries. Therefore, the transect sample survey estimate probably did not have large errors due to inefficient sampling of large estuarine concentrations. In 1985, a total of 481 whales were counted on the eastern Hudson Bay coastal survey, including concentrations in Richmond Gulf and in the estuaries of both the Little Whale and Nastapoca rivers (Smith and Hammill 1986), and land-based observations in 1984 counted as many as 200 individuals in the Nastapoca estuary (on 24 August: Caron and Smith, 1990) compared with the 1993 maximum of 53.

Transect sample survey and nearshore total-count indices apparently corroborate the finding that numbers in

Table 4

Distribution of beluga whale observations and estimated numbers of beluga whales in eastern Hudson Bay between the Nunavik area, the Nunavut Settlement Area, and the Equal Use and Occupancy Area.

	Observations (%)	Mean number per observation	Estimated numbers (%)
Nunavik area	23 (36)	4.2	774 (71)
Nunavut Settlement Area	25 (39)	1.4	211 (19)
Equal Use and Occupancy Area	16 (25)	1.2	111 (10)

eastern Hudson Bay were not larger in 1993 than they had been in 1984–5, but instead were very likely lower.

Sightings of beluga whales in eastern Hudson Bay showed that they were widely distributed in the shallow water between the mainland coast and the Belcher Islands (Fig. 4). Thirty-six percent of sightings were outside the areas defined by the Nunavut Agreement (Table 4), but these were on average the larger groups, and represented 71% of the total numbers. Beluga whales were distributed also around the Belcher Islands, particularly to the north, and as far west as the survey extended. There was no evidence of a discontinuity in the east–west distribution. The survey results were consistent with the hypothesis of a single continuous population distributed from the coast out to the survey limit. However, it is not known for sure whether all the beluga whales in the study area were among those that frequent the estuaries on the eastern Hudson Bay mainland coast, nor whether they would be available to hunters there. It remains possible that the beluga whales using those estuaries are only a fraction of the total numbers counted in the survey area. The question of single or multiple summering stocks in eastern Hudson Bay is important in designing strategies for managing exploitation by residents of the communities on the Belcher Islands and on the eastern Hudson Bay coast; aerial survey results alone can not provide conclusive answers.

The north–south extent of the sightings in eastern Hudson Bay was limited, as in 1985; no beluga whales were seen on the northernmost transects, and there was no continuous distribution extending into areas farther north. There are no large estuaries to attract summering beluga whales to the eastern Hudson Bay coast north of the Nastapoca River, and there are no reports, even anecdotal, of beluga whales spending the summer in those areas. Thus it is unlikely that significant additional numbers would have been detected if this survey had extended farther north.

The estimate of numbers in Ungava Bay was uncertain. In James Bay, beluga whale groups were widely distributed. In Hudson Bay, densities were lower, but sightings were frequent and widely distributed. In Ungava Bay very few beluga whales were seen, indicating a very low density. Population estimates from the transect surveys, based on 0 or 1 sighting per survey, are imprecise, but small, of the same order as the highest daily total counts on survey and reconnaissance flights combined, and consistent with the maximum of about 25 beluga whales in the Mucalic River estuary in summer estimated by Finley et al. (1982). The present survey could have resighted the same small group of about that size, or subgroups of it, on different flights. The largest sighting from land was 17 individuals, on 24 August 1993. Smith and Hammill (1986) surveyed Ungava Bay in 1985, and saw few beluga whales; they were unable to make a population estimate.

Most sightings were made in and near the Whale River estuary, but a few, small, scattered groups were also sighted elsewhere in Ungava Bay (Table 3). Residents of the area see beluga whales in summer, but not in large numbers and not all the time (Brooke[6]; Brooke[7]; Portnoff[8]). Ungava Bay communities capture beluga whales in most years, but often outside the bay and outside the season when they inhabit their summer grounds. Neither survey results nor harvest statistics provided a basis for considering a trend in summering stock size.

Estimates from line-transect survey analysis were conditional on the use of the Richards curve as a sighting curve. Both the hazard-rate curve and the normal curve fitted the data worse. Maximum detection was not obtained until 470 m from the aircraft, owing to its having flat windows. Similar visibility restrictions have been estimated in other surveys. In a line-transect aerial survey of narwhals in Scoresby Sund, in which the survey plane had flat windows, there were poor sighting rates out to a sighting angle of about 40° from the vertical (Larsen et al., 1994) and in an aerial survey of cetaceans in the Gulf of St Lawrence, in which the survey aircraft had shallow bubble windows, maximum detection was not achieved until 35° from the vertical (Kingsley and Reeves 1998). The loss of visibility close to the aircraft militates in favour of lower flying heights if surveys must be carried out in flat-windowed aircraft and raises concerns about detection, if the

[6] Brooke, L. F. No date. A report on the 1994 Nunavik beluga and walrus subsistence harvest study. Unpublished report prepared for the Department of Fisheries and Oceans, 104, rue Dalhousie, Quebec P.Q. G1K 4B8, Canada, 29 p.

[7] Brooke, L. F. No date. A report on the 1995 Nunavik beluga a[nd] walrus subsistence harvest study. Unpublished report prepared for the Department of Fisheries and Oceans, 104, rue Dalhousie, Quebec P.Q. G1K 4B8, Canada, 29 p.

[8] Portnoff, M. 1994. The 1993 Nunavik beluga whale and walrus subsistence harvest study. Report prepared for the Department of Fisheries and Oceans, 104, rue Dalhousie, Quebec P.Q. G1K 4B8, Canada by Nunavik Graphics, Montreal, 61 p.

maximum visibility is not reached until so far away from the aircraft. The present results have not been corrected for detection bias, but Harwood et al. (1996) estimated, from paired-observer data, that it would be appropriate to add about 40% to correct for detection bias at the peak of the sighting curve even when using bubble windows.

The sightings curve fitted to the present data set has a shoulder at 670 m, and the width of the maximum-visibility strip, a critical determinant of the precision of the survey, was small. Larsen at al. (1994, Fig. 2) noted a marked drop in visibility of narwhal from the air beyond 823 m. In other studies, visibility of beluga whales dropped off beyond about 600 m from the aircraft (Norton and Harwood 1985), and by 600 m visibility of small cetaceans was less than 40% of maximum (Kingsley and Reeves 1998); both these surveys were flown lower than the 457 m of the present survey.

Estimates were not been corrected for diving beluga whales, but instead were conservative estimates of surface-visible beluga whales. Corrections to counts of beluga whales for diving have been estimated from visual records of their appearance and disappearance (Brodie, 1971; Sergeant, 1973; Fraker, 1980; Gauthier, 1999), by recording surface signals from attached VHF radio transmitters (Frost et al., 1985), and by studying diving behavior with attached pressure recorders (Martin and Smith, 1992; Richard et al., 1997; Heide-Jørgensen et al., 1998; Kingsley, unpubl. data). Early studies (Brodie, 1971; Sergeant, 1973) were restricted to nearshore areas. Correction estimates have ranged from adding 40% (Brodie, 1971) to adding 200% (Sergeant, 1973). A correction for eastern Hudson Bay, deduced from satellite-tag data on five beluga whales tagged in 1993, was about 80%, but there was a wide margin of uncertainty. This value was similar to values estimated for beluga whales summering in other waters of the Canadian Arctic (Martin and Smith, 1992; Richard et al., 1997; Heide-Jørgensen et al., 1998).

Large sampling variability is common in beluga whale surveys, the species being gregarious. Most of the error variance for individual strata in the line-transect survey was due to uncertainty in encounter rate, especially in the northern Hudson Bay stratum, where a few large groups were seen on a few transects. Overall, the error coefficient of variation was 23%, of which about 2/3 was due to uncertainty in encounter rate. The jack-knife bias reduction (Efron, 1982) reduced the estimate of the survey expansion factor by only 1%, from 0.583 /nmi to 0.575 /nmi.

Acknowledgments

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THE PAPER AND INK USED IN THE ORIGINAL PUBLICATION MAY AFFECT THE QUALITY OF THE MICROFORM EDITION.

Age and growth of cutlassfishes, *Trichiurus* spp., from the South China Sea

Kai Yin Kwok
I-Hsun Ni

Department of Biology
Hong Kong University of Science & Technology
Hong Kong SAR, China
E-mail address (for I-H Ni, contact author): boniih@ust.hk

Abstract—Age and growth of two species of cutlassfishes, *Trichiurus* spp. (Trichiuridae), from the South China Sea were examined. Between December 1996 and November 1997, 1495 specimens were collected from coastal waters near Hong Kong. Two species, *Trichiurus lepturus* and *T. nanhaiensis*, were harvested and ages of specimens were estimated by using transverse sections of the sagittal otoliths. Opaque growth rings were verified to have formed annually during February. Lee's phenomenon was not observed for either species, although *T. lepturus* tended to display reverse Lee's phenomenon. Otolith weight was linearly related to age, and accounted for about 72% and 76% of the variation in age (t) for *T. lepturus* and *T. nanhaiensis*, respectively, comparable to the von Bertalanffy growth models in preanal length (PL). For older fish, otolith weight provided a more precise estimate of age than preanal length. Preanal length and age were fitted to the von Bertalanffy growth model by nonlinear regression, resulting in

$$PL\ (\text{mm}) = 589\{1 - e^{[-0.168\,(t\,+\,2.682)]}\}$$
(*T. lepturus*);

$$PL\ (\text{mm}) = 602\{1 - e^{[-0.207\,(t\,+\,2.044)]}\}$$
(*T. nanhaiensis*).

Growth in length of the two species was significantly different (ANCOVA, $F_{2,1245}$=169.69, P<0.001).

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The cutlassfish, *Trichiurus lepturus* Linnaeus 1758, occurs throughout tropical and temperate waters of the world, between latitude 60°N and 45°S (Froese and Pauly, 1997). World harvests are approximately 750,000 tonnes annually and China lands about 80% (600,000 tonnes) (Claus, 1995). In terms of weight, cutlassfish is the most important commercial marine fish species in China (Luo, 1991) and has accounted for about 10% to 20% of the total marine fish catch. It is caught in all Chinese seas, the Bo Hai, the Yellow Sea, the East China Sea, and the South China Sea (Jiang et al., 1991), and about 15% of the catch comes from the South China Sea (Fig. 1) (Liu, 1996). Cutlassfish is used as food fish and is caught mainly by bottom trawling (Luo, 1991) and in lower amounts by longline, hand line, gill net, drift net and purse seine (Chen and Liu, 1982).

Age and growth studies and their derived growth parameters are indispensable in determining stock dynamics (Brouard et al., 1984). Numerous age and growth studies of *T. lepturus* have been conducted over the past few decades (Table 1); however, most research has focused on northern populations in the East China Sea, the Yellow Sea, and the Bo Hai. Similar work on populations in the South China Sea has not been available.

Three species of trichiurids occur in the South China Sea, *T. lepturus*, *T. nanhaiensis* (Wang and Xu, 1992, in Wang et al., 1992), and *T. brevis* (Wang and You, 1992, in Wang et al., 1992), whereas only one species, *T. lepturus*, occurs in the waters of China farther north (Wang et al., 1992, 1993, 1994). Populations of *T. lepturus* in the Bo Hai, the Yellow Sea, and the East China Sea suffer from overfishing (Lin, 1985; Du et al., 1988; Ma and Xu, 1989; Luo, 1991; Ye and Rosenberg, 1991; Xu et al., 1994). It is harvested only in the Bo Hai and the Yellow Sea as bycatch in other fisheries (Lin, 1985). The condition of trichiurid stocks in the South China Sea remains unclear.

Numerous methods have been used to age trichiurids. The length-frequency method has proven useful in India (Narasimham, 1976; Chakraborty, 1990) and the Philippines (Ingles and Pauly, 1984). Yet, hard parts such as whole or sectioned otoliths and vertebral centra are most frequently used to age cutlassfish (Table 1). Measuring otolith weight or otolith size may be a cost-effective method for aging some fishes (Barbieri et al., 1994; Ferreira and Russ, 1994; Worthington et al., 1995). Although sectioned otoliths are reliable for aging fish, the method is time consuming and expensive (Beckman et al., 1991).

The aims of our study were 1) to validate age estimates by using transverse sections of sagittal otoliths; 2) to verify Lee's phenomenon; 3) to evaluate the potential of using otolith size and weight to estimate age; 4) to fit the age-length data to the von Bertalanffy growth model; and 5) to provide age-growth information for management of cutlassfish resources from the South China Sea.

Materials and methods

Between December 1996 and November 1997, 960 specimens (preanal length [PL] range:138–468 mm; PL=the tip of the lower jaw with the mouth closed to the middle of anus) of *T. lepturus*, and 535 specimens (PL range:253–551

mm) of *T. nanhaiensis* were obtained from commercial catches in the coastal waters of Hong Kong. Commercial gears included longlines, purse seines and bottom trawls. Fresh specimens were placed on ice, transported to the laboratory, and identified by using the diagnostic key of Wang et al. (1992, 1993): if the frontal bone split laterally, specimens were identified as *T. lepturus*, otherwise *T. nanhaiensis*. Preanal lengths were measured to the nearest mm. Specimens were blotted dry and weighed (whole and gutted) to the nearest 0.01 g. To estimate the relationship between PL and gutted weight (W), the variables were log-transformed to meet the assumptions of normality and homogeneous variance. A linear version of the power function: $W\,(g) = a\,PL^b$ (mm) was fitted to the data.

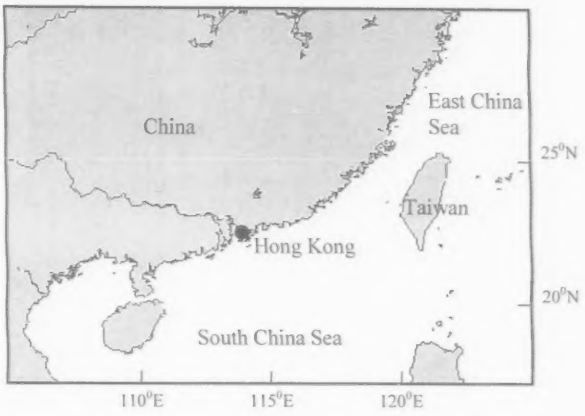

Figure 1
The South China Sea and surrounding area.

Distinct growth rings on whole otoliths and vertebral centra were ill-defined. Transverse sections of sagittal otolith yielded "readable" growth rings; the latter were chosen as aging tools. Left and right sagittae were weighed independently to the nearest 0.01 mg after being oven dried at 40°C for 30 min. Otolith length (OL) was measured to the nearest 0.05 mm with calipers. Sagittal otoliths were embedded in resin and sectioned transversely through the nucleus with a low-speed saw. Up to five sections, 0.3 to 0.5 mm thick, were made from each otolith to ensure that at least one passed through the center of the nucleus. Sections were then ground with 1000- and 1200-grit sand paper, mounted on glass slides with clear fingernail polish, and examined with a compound microscope at 40× magnification with transmitted light. The relative age in years was determined by counting the number of opaque growth rings on the dorsal side of the sectioned otoliths (Fig. 2). Thirty-five pairs of sectioned otoliths of both species were processed. No differences in the number of growth rings were found in left and right sections of each pair. Thereafter, the right sagitta was used for age determination.

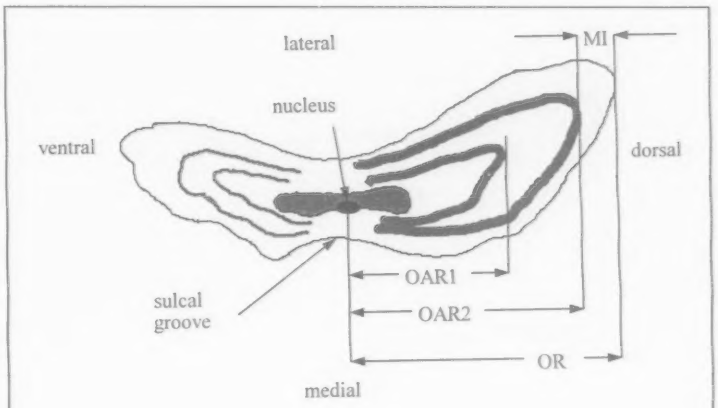

Figure 2
Schematic diagram of a transversely sectioned sagittal otolith of cutlassfishes, *Trichiurus* spp. MI = marginal increment, OAR1 = first otolith annular radius, OAR2 = second otolith annular radius, OR = otolith radius.

Otoliths were read twice (one month apart) in a random order, with no knowledge of fish length or species. Precision was measured by the percentage of agreement between readings (Lowerre-Barbieri et al., 1994). Deviations were counted a third time. Only counts with at least two agreements were used in subsequent analyses. Marginal increment method was used to validate the reading of annuli. Otolith radius (OR), otolith annular radius (OAR), and marginal increment (MI) (Fig. 2) were measured with an ocular micrometer to the nearest 0.025 mm.

The tendency for older fish to reflect smaller back-calculated length at earlier ages than measured length is known as Lee's phenomenon (Smith, 1983), and is related to size-selective mortality (Boehlert et al., 1989). To evaluate this phenomenon, the mean otolith annular radius (MOAR) for each annulus of the same age group was calculated, and the MOAR for each annulus of different age groups was plotted against the age group (Yamaguchi et al., 1990). Thus, we determined if older fish demonstrated slower growth of hard parts at younger ages, i.e. true Lee's phenomenon (Smale and Taylor, 1987). The ANOVA test was used to compare MOARs among different age groups.

Multiple linear-regression models were fitted in a stepwise manner to predict age from otolith weight and length. Variables were log-transformed to meet the assumptions of normality and homogeneous variance. A paired-sample *t*-test showed no significant difference between left and right sagittal otoliths in terms of weight (*T. lepturus*:

Table 1

Summary of age and growth studies of *Trichiurus lepturus*. A = Autumn brood; F = female; L_∞ = in preanal length; M = male; MI = marginal increment; otolith = sagittal otolith; S = spring brood;

Country	Study area	Study period	Sample size	Sex and brood	Aging and growth methods	Validation method	Growth parameters			Authors
							k(per yr)	L_∞(mm)	t_0(yr)	
China	East China Sea, Yellow Sea & Bo Hai	1954–57	1472		whole otolith, Ford–Walford plot	MI	0.4083	455.7	0.4400	Misu, 1958, 1964
China	East China Sea	1968–69	869		sectioned otolith, Ford–Walford plot	MI	0.1390	766.0	–0.2660	Hamada, 1971
China	East China Sea north	1977–78	3418		sectioned otolith, Ford–Walford plot	MI	0.2928	553.2	–0.6806	Wu et al., 1985a, 1985b
China	Yellow Sea	1964			whole otolith,		0.1100	708.0	–2.8200	Lin and Zhang, 1981
China	Bo Hai	1964			Ford–Walford plot		0.1100	658.0	–2.9100	
China	Yellow Sea & Bo Hai	1962–63	492		whole otolith,	MI	0.4380	501.0	–0.0607	Hong, 1980
Japan	Kii Channel	1972–74	3739		whole otolith, ford–Walford plot	MI	0.2610	568.3	–0.6435	Sakamoto, 1976
Japan	Kumano– Nada	1978–79	213	S	whole otolith,	MI	0.3960	483.0	–0.4350	Suzuki and Kimura,
				A	ford–Walford plot		0.5240	439.0	0.5280	1980
Japan	Suruga Bay	1965	505		whole otolith, ford–Walford plot	MI	0.2886	433.9	–0.4130	Kosaka et al., 1967
Japan	Kagoshima Bay	1993–94	292	F	whole otolith,	MI	0.1670	629.0	–1.7910	El–Haweet and Ozawa,
				M	ford–Walford plot		0.2160	481.0	–1.9750	1996[1]
Japan	Tsushima waters	1967–87	9592	S, F	whole otolith,	MI	0.4090	502.5	–0.4910	Hanabuchi, 1989
				S, M	ford–Walford plot		0.4810	438.7	–0.4580	
				A, F			0.4590	465.1	–0.2200	
				A, M			0.5530	400.7	–0.1960	
China	Taiwan Strait	1962–64	3319		vertebral centrum, Ford–Walford plot	MI	0.2920	477.4	–0.6340	Du et al., 1988
Taiwan	coastal sea (E)	1976–77	154		whole otolith, Ford–Walford plot	MI	0.2710	502.0	–0.2200	Chen and Lee, 1982
Taiwan	coastal sea (SW)	1976–77	341		whole otolith, Ford–Walford plot	MI	0.2890	550.0	–0.7600	Chen and Lee, 1982

[1] Studies used species name *T. japonicus* which was a junior synonym of *T. lepturus* (after Froese and Pauly, 1997).

t=–0.097, df=917, P>0.90; *T. nanhaiensis*: t=–0.762, df=518, P>0.44) and length (*T. lepturus*: t=–0.471, df=916, P>0.45; *T. nanhaiensis*: t=–0.689, df=523, P>0.49). Therefore, average otolith length and weight were used in the analyses. For all the linear regressions mentioned above, analysis of covariance (ANCOVA) was used to compare regressions between sexes and species.

We assigned 1 May and 1 June as the birth dates for *T. lepturus* and *T. nanhaiensis*, respectively (Kwok and Ni, 1999). Relative ages derived from aging were then converted to absolute ages. Von Bertalanffy growth curves were fitted by nonlinear regression on age and preanal length data (SPSS vers. 7.5). The von Bertalanffy growth equation for length is

$$PL_t = PL_\infty \{1 - e^{[-k\,(t - t_0)]}\},$$

where PL_∞ = the asymptotic length;
k = growth coefficient; and
t_0 = the hypothetical age at zero length.

Plots of residuals from regression models were used to check the assumption of normality. ANCOVA was used to compare log-transformed age-at-length regressions between sexes and species.

Results

The preanal length (mm) and gutted weight (g) regression models were significantly different between sexes (ANCOVA: *T. lepturus*: $F_{2,932}$=4.00, P<0.05; *T. nanhaiensis*: $F_{2,530}$=3.34, P<0.05) and species (ANCOVA: $F_{2,1466}$=83.76, P<0.001). The regression models were

T. lepturus
males:
$W = 1.513 \times 10^{-4}\ PL^{2.571}$ (n=212, r^2=0.9777, P<0.001);
females:
$W = 1.748 \times 10^{-4}\ PL^{2.549}$ (n=724, r^2=0.9761, P<0.001);
sexes combined:
$W = 1.624 \times 10^{-4}\ PL^{2.561}$ (n=936, r^2=0.9771, P<0.001);

T. nanhaiensis
males:
$W = 3.363 \times 10^{-5}\ PL^{2.846}$ (n=282, r^2=0.8506, P<0.001);
females:
$W = 6.553 \times 10^{-5}\ PL^{2.729}$ (n=252, r^2=0.9299, P<0.001);
sexes combined:
$W = 5.672 \times 10^{-5}\ PL^{2.755}$ (n=534, r^2=0.8968, P<0.001).

Sectioned sagittae of both species had an opaque nucleus located above the sulcal groove toward the dorsum. The nucleus was surrounded by a pattern of alternating wide, translucent zones and thin, opaque zones; the latter were considered annuli (Fig. 3). Annuli were distinct on the dorsum of the sections but were usually indecipherable on the ventral side. A total of 757 and 534 otoliths were embedded in resin and sectioned for *T. lepturus* and *T. nanhaiensis*, respectively. Of these, 33 (4.3%) and 9 (1.7%) were unreadable, and the percentage agreement between the two readings for each species was 95.4% and 92.7%, respectively.

The least marginal increment values (Fig. 4) occurred in February for both species, suggesting that one growth ring (annulus) formed each year. Only specimens age 1–4 were included in the analyses because older fish were rare in our collections. The mean otolith annular radius (MOAR) of the first annulus (ANOVA: $F_{5,582}$=3.046, P<0.05) and third annulus (ANOVA: $F_{3,80}$=4.024, P<0.05) of *T. lepturus* were significantly different among different age groups (Fig. 5); MOARs increased slightly with older age groups. However, no particular trend was found with regard to the MOARs of *T. nanhaiensis* (Fig. 5). Lee's phenomenon was not evident for either species, although reverse Lee's phenomenon was possible for *T. lepturus*.

Otolith weight accounted for 68.7% and 68.9% (Table 2) of the variability in age for *T. lepturus* and *T. nanhaiensis*, respectively. A negligible amount of the remaining variability was explained by considering otolith length in addition to otolith weight. The otolith weight-age regression was improved by fitting the untreated variables (otolith weight and age) with simple linear regression models:

T. lepturus:
$OW = 6.3533 + 5.2913Age$ (n=718, r^2=0.7168, P<0.001);
T. nanhaiensis:
$OW = 6.3921 + 3.6850Age$ (n=515, r^2=0.7561, P<0.001).

These regression results suggest a linear relationship between otolith weight and age (Fig. 6). The regression models were significantly different between the two species (ANCOVA: $F_{2,1229}$=224.17, P<0.001). Normal probability and residual plots showed that the regressions complied with the assumptions of normality and homogeneous variance.

Von Bertalanffy growth equations for both species were

T. lepturus
males:
$PL = 755.2\ \{1 - e^{[-0.116\,(t\,+\,2.737)]}\}$ (n=146, r^2=0.684, P<0.001);
females:
$PL = 601.4\ \{1 - e^{[-0.158\,(t\,+\,2.850)]}\}$ (n=578, r^2=0.765, P<0.001);
sexes combined:
$PL = 589.1\ \{1 - e^{[-0.168\,(t\,+\,2.682)]}\}$ (n=724, r^2=0.749, P<0.001);

T. nanhaiensis
males:
$PL = 501.7\ \{1 - e^{[-0.306\,(t\,+\,1.673)]}\}$ (n=281, r^2=0.682, P<0.001);
females:
$PL = 612.6\ \{1 - e^{[-0.220\,(t\,+\,1.792)]}\}$ (n=244, r^2=0.726, P<0.001);
sexes combined:
$PL = 602.1\ \{1 - e^{[-0.207\,(t\,+\,2.044)]}\}$ (n=525, r^2=0.699, P<0.001).

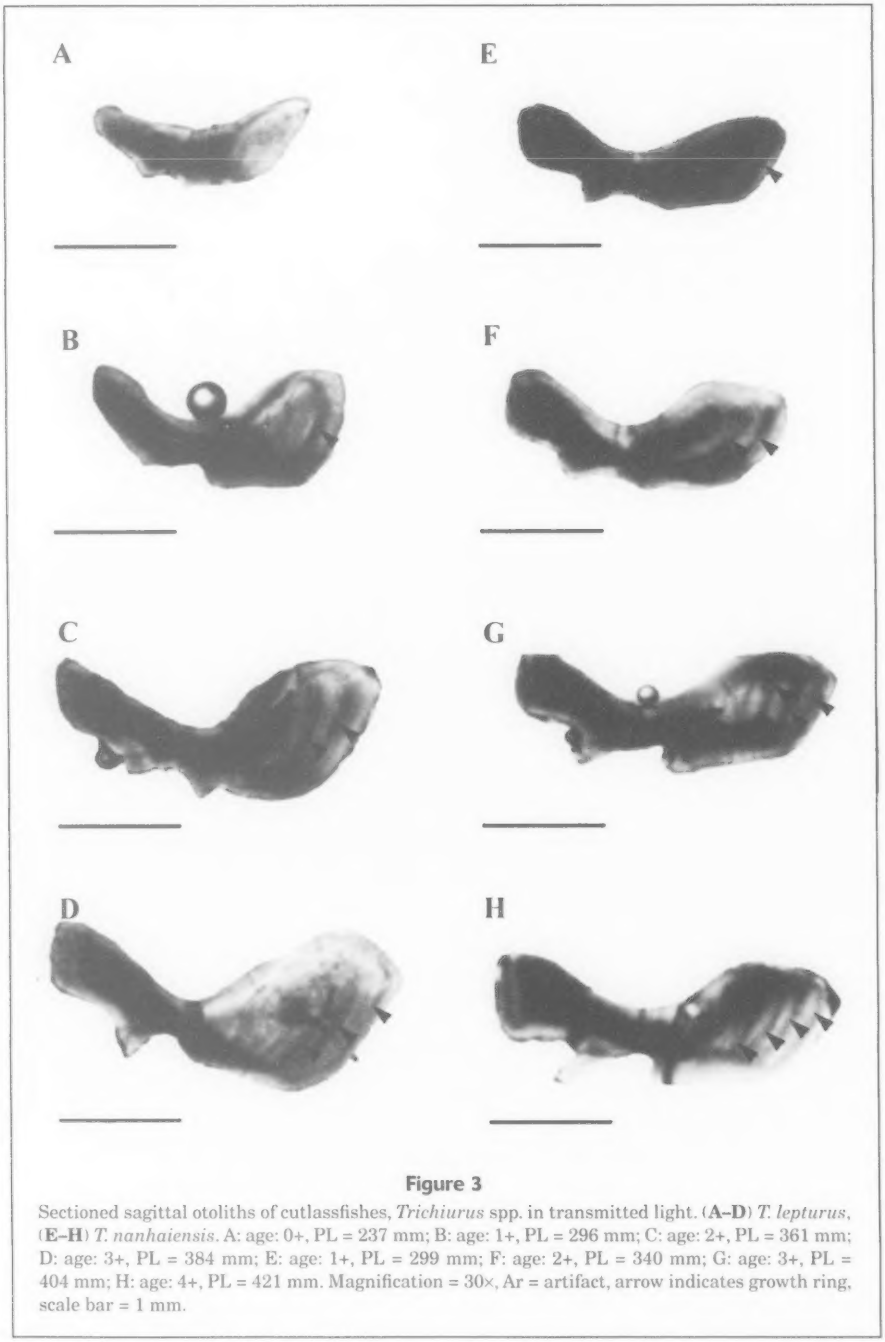

Figure 3

Sectioned sagittal otoliths of cutlassfishes, *Trichiurus* spp. in transmitted light. (**A–D**) *T. lepturus*, (**E–H**) *T. nanhaiensis*. A: age: 0+, PL = 237 mm; B: age: 1+, PL = 296 mm; C: age: 2+, PL = 361 mm; D: age: 3+, PL = 384 mm; E: age: 1+, PL = 299 mm; F: age: 2+, PL = 340 mm; G: age: 3+, PL = 404 mm; H: age: 4+, PL = 421 mm. Magnification = 30×, Ar = artifact, arrow indicates growth ring, scale bar = 1 mm.

Von Bertalanffy growth curves for sexes combined are depicted in Figure 7. No systematic trend was found in the residual plots for all regressions. The t_{max} (age at 95% of asymptotic length) of *T. lepturus* and *T. nanhaiensis* were 15.1 and 12.4 years, respectively. The W_{∞} (asymptotic weight: estimated by substituting PL_{∞} to the preanal length-weight equations) of *T. lepturus* and *T. nanhaiensis* were 2025 g and 2585 g, respectively. Log-transformed age-at-length regressions were significantly different between sexes (ANCOVA: *T. lepturus*:

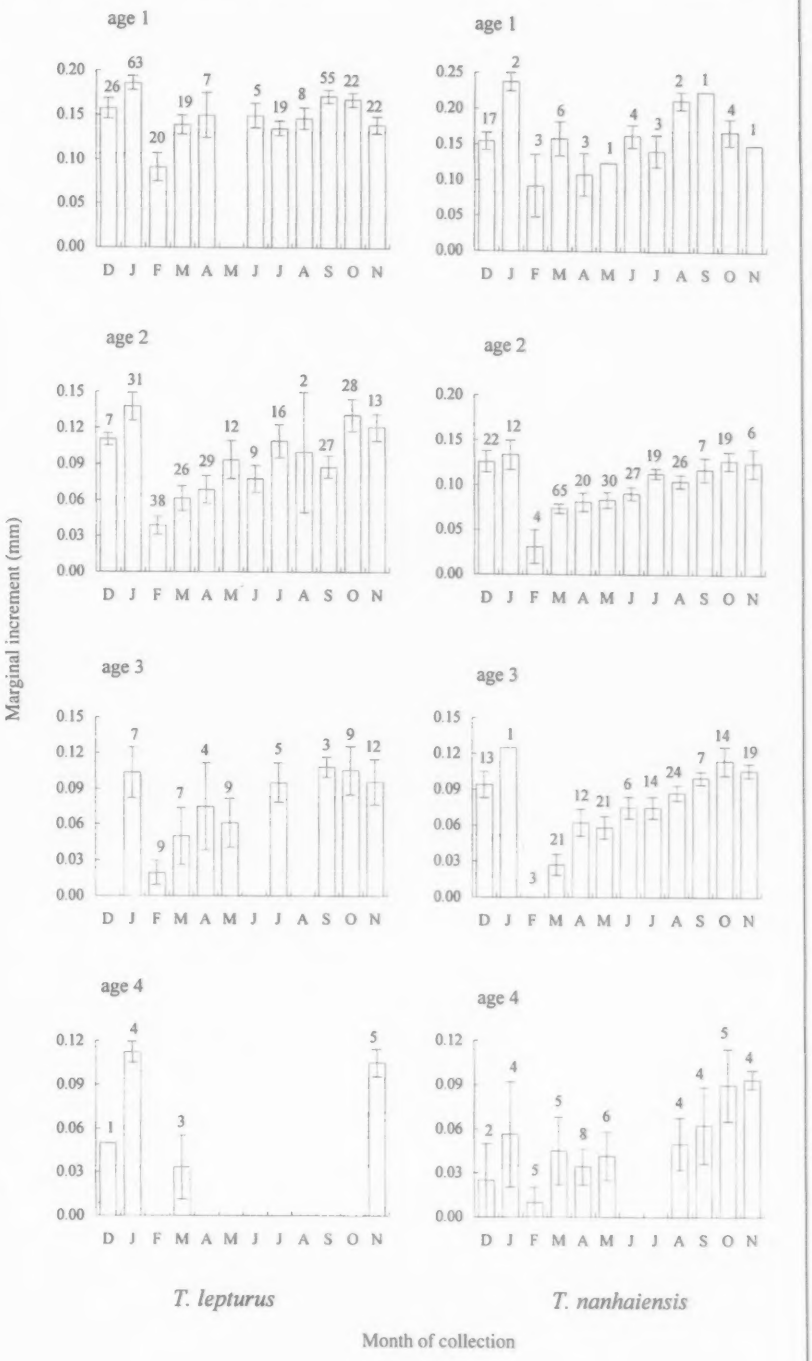

Figure 4

Mean monthly otolith marginal increment for *T. lepturus* (left panel) and *T. nanhaiensis* (right panel). Vertical bars are 1 SE, numbers on the top of vertical bars are sample sizes.

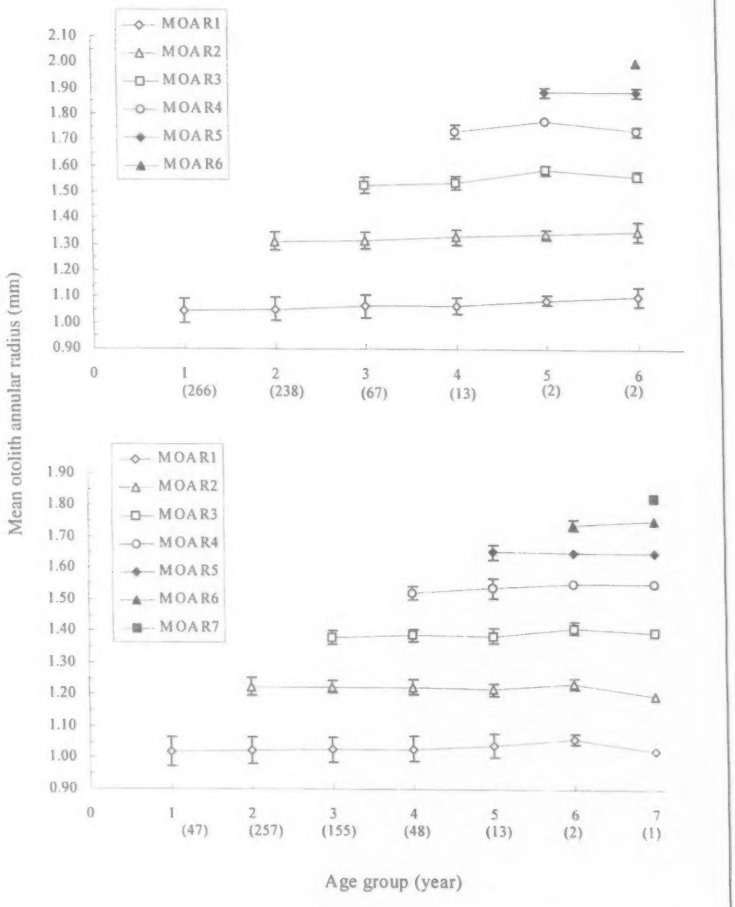

Figure 5

The relationship between mean otolith annular radius (MOAR) and age group for *Trichiurus lepturus* (top panel) and *T. nanhaiensis* (bottom panel). Vertical bars are 1 SE, numbers in parentheses are sample sizes.

$F_{2,720}$=4.39, P<0.05; *T. nanhaiensis*: $F_{2,521}$=23.78, P<0.001) and species (ANCOVA: $F_{2,1245}$=169.69, P<0.001).

Discussion

Our aging study of cutlassfishes from the South China Sea was successful in that we 1) found distinct growth rings on sectional sagittal otolith, 2) had excellent precision in independent ring counts, and 3) used marginal increment analyses to validate our aging method. In general, cutlassfishes from the northern seas of China (Misu, 1958, 1964; Hamada, 1971; Sakamoto, 1976; Hong, 1980; Wu et al., 1985a; Du et al., 1988; Hanabuchi, 1989; El-Haweet and Ozawa, 1996) and the South China Sea (our study) deposit annuli in late winter or early spring, suggesting that ring formation likely occurs in response to reduced water temperatures and is not correlated with peak spawning as indicated in Chen and Lee (1982). Summer is the peak spawning period of *T. lepturus* and *T. nanhaiensis* in the South China Sea (Kwok and Ni, 1999).

El-Haweet and Ozawa (1996) questioned whether Lee's phenomenon existed in a trichiurid population from Japan, having found no indication of Lee's or reverse Lee's phenomenon. We found that *T. lepturus* may exhibit reverse Lee's phenomenon, which suggests that *T. lepturus* are not overfished in the South China Sea or that fishing mortality is not size-selective, or that both situations may apply. Alternatively, fast growing individuals in the *T. lepturus* population may have greater chances of survival and attain older ages.

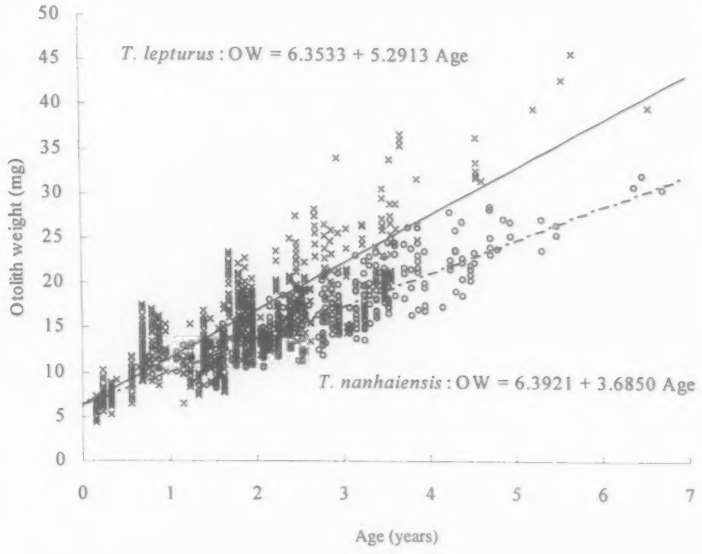

Figure 6

Regression model between otolith weight and age for *Trichiurus* spp. Solid line (regression line) and crosses (raw data): *T. lepturus*. Dotted line (regression line) and circles (raw data): *T. nanhaiensis*.

Table 2

Regression coefficients and statistics on multiple-regression models of age for cutlassfishes, *Trichiurus* spp. Variables were log-transformed for analyses.

Variable	Coefficient	SE	*P*	Partial r^2
T. lepturus (n=718)				
one-variable model (r^2=0.687)				
intercept	–4.404	0.108	<0.0001	
otolith weight	1.629	0.041	<0.0001	0.687
two-variable model (r^2=0.696)				
intercept	–5.922	0.430	<0.0001	
otolith weight	0.966	0.153	<0.0001	0.053
otolith length	2.076	0.461	<0.0001	0.028
T. nanhaiensis (n=515)				
one-variable model (r^2=0.689)				
intercept	–2.692	0.107	<0.0001	
otolith weight	1.305	0.039	<0.0001	0.689
two-variable model (r^2=0.690)				
intercept	–3.068	0.227	<0.0001	
otolith weight	1.123	0.105	<0.0001	0.183
otolith length	0.476	0.255	>0.05	0.007

The linear relation between otolith weight and age (Fig. 6) indicates that cutlassfish otoliths continuously increase in weight with age. The regression models explain 72% and 76% of the variance for *T. lepturus* and *T. nanhaiensis*, respectively, comparable to the von Bertalanffy growth model in preanal length. Thus, otolith weight pro-

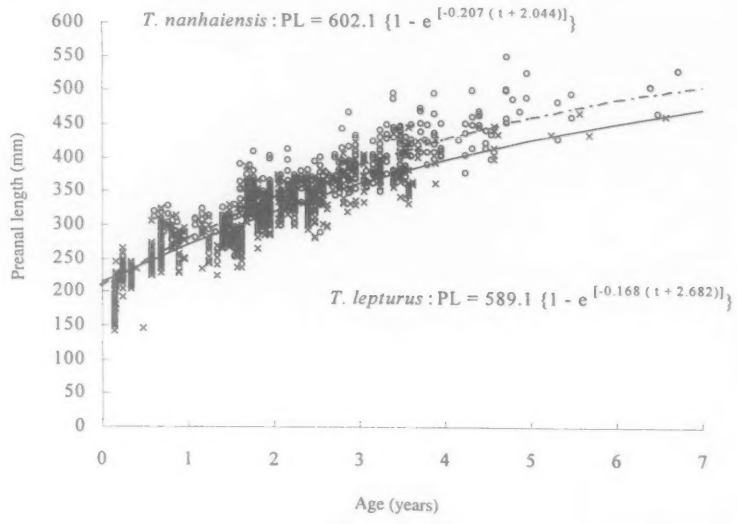

Figure 7

The von Bertalanffy growth curve for *Trichiurus* spp. Solid line (regression line) and crosses (raw data): *T. lepturus*. Dotted line (regression line) and circles (raw data): *T. nanhaiensis*.

vides a more precise estimate of age in older fish. Use of otolith weight to estimate age should be done with caution because these relationships have been shown to be population specific (Worthington et al., 1995).

This study is the first application of nonlinear regression in deriving a von Bertalanffy growth model for the cutlassfish; previously Ford-Walford plots were the most common method. The shortcomings associated with that method include 1) weighing problems due to different sample sizes of each age group; 2) a failure in providing variance-covariance for comparisons; 3) none of the raw data are used (Liu and Yeh, 1991); and 4) a reliance on back-calculated body length, which is usually estimated from the linear regression between hardpart dimension (e.g. otolith radius) and body length. Unfortunately, the growth of otoliths has been shown to be independent of somatic growth (Beckman et al., 1991; Barbieri et al., 1994), i.e. growth of body length ceases with age, while growth of hard parts continue. In comparison, our application of nonlinear regression analysis can avoid all these problems.

Basic growth parameters for these two populations of trichiurids in the South China Sea showed lower growth coefficients and higher asymptotic length, i.e. specimens reached maximum size at a slower pace than other trichiurids from the western Pacific Ocean (Table 1). This finding may be real or may reflect different methods employed for estimating growth.

In our comparison of the two species, *T. nanhaiensis* possessed a higher growth coefficient (k) than *T. lepturus*. Male *T. lepturus* had a lower growth coefficient but attained larger asymptotic size (PL_∞) than did female *T. lepturus*, whereas the opposite held true for *T. nanhaiensis*.

We provide basic growth parameters for use in the study of stock dynamics of trichiurids in the South China Sea. A formal stock assessment should be conducted with special emphasis on establishing an ecologically sustainable cutlassfish fishery in the South China Sea to prevent overfishing, or even fishery collapse, as has occurred in the northern populations of trichiurids.

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Monitoring protocol for Sacramento River winter chinook salmon, *Oncorhynchus tshawytscha*: application of statistical power analysis to recovery of an endangered species*

Steven T. Lindley
Michael S. Mohr
Michael H. Prager

Santa Cruz/Tiburon Laboratory
Southwest Fisheries Science Center
National Marine Fisheries Service, NOAA
3150 Paradise Drive
Tiburon, California 94920

E-mail address (for S. T. Lindley): Steve.Lindley@noaa.gov

Abstract—When monitoring endangered species, natural resource managers require a recovery benchmark and a statistical procedure to test whether the benchmark has been met. We applied statistical power analysis to devise such a procedure for the endangered Sacramento River winter chinook salmon (*Oncorhynchus tshawytscha*). Winter chinook salmon management currently focuses on population growth rate, and our procedure used a Student's *t*-test to evaluate whether the average population growth rate is significantly lower than the management goal of 0.57 per generation. In the test, the null hypothesis was that the growth rate was not lower than the desired rate. In contrast to the usual hypothesis-testing framework, our procedure did not control for the type-I error rate. Instead, it controlled for the statistical power (the complement of the type-II error rate) and uses the resulting type-I error rate, computed from the sample size and other information, for the test. This procedure is conservative for winter chinook salmon in that, if all assumptions are met, it provides the specified level of assurance of detecting dangerously low population growth rates.

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Fish. Bull. 98:759–766 (2000).

The Sacramento River winter chinook salmon is listed as an endangered species under the U.S. Endangered Species Act (ESA). The historical spawning grounds of the winter chinook salmon were in upper tributaries of the Sacramento River, including the Upper Sacramento, Pit, and McCloud Rivers (Fig. 1). The completion of Shasta and Keswick Dams in the 1940s blocked access to these spawning grounds, although populations had already declined from historic levels owing to habitat destruction in the upper tributaries (Fisher, 1994). Quantitative winter chinook salmon population size estimates began in 1967 when the Red Bluff Diversion Dam (RBDD), a flashboard dam with three fish ladders, was completed. Since the completion of RBDD, winter chinook salmon spawning runs have declined from over 100,000 adults to a few hundred adults in the 1980s (Fig. 2; Williams and Williams, 1991).

The winter chinook salmon population remains extremely depleted. The California Fish and Game Commission listed the population as a "candidate" species under California's Endangered Species Act in 1988 and declared it endangered under that Act in 1989. The National Marine Fisheries Service (NMFS) declared the species "threatened" under the federal ESA in the same year, and it was declared "endangered" in 1994. NMFS has taken numerous regulatory actions under the ESA to improve winter chinook salmon survival, including changes in the regulations governing California's ocean salmon fisheries.[1]

In 1997, NMFS required that future ocean fishery harvest regulations be designed to achieve at least a 31% increase in the winter chinook salmon average cohort replacement rate over that observed in 1989–93.[2] Because winter chinook salmon females spawn predominantly at age 3 (Fisher, 1994), the cohort replacement rate in year i is, for simplicity, defined as $R_i = N_i/N_{i-3}$, where N_i is the number of adult spawners passing RBDD in year i. For statistical modeling purposes, it is convenient to express this cohort replacement rate on the log scale, $r_i = \log(R_i)$, and refer

* Contribution 103 of the Santa Cruz/Tiburon laboratory, Southwest Fisheries Science Center, National Marine Fisheries Service, NOAA, 3150 Paradise Drive, Tiburon, CA 94920.

[1] Pacific Fishery Management Council. 1998. Review of 1997 ocean salmon fisheries. [Available from Pacific Fishery Management Council, 2130 SW Fifth Avenue, Suite 224, Portland, OR 97201.]

[2] NMFS, 1996. Endangered Species Act-Section 7: Consultation. Biological opinion. The fishery management plan for commercial and recreational salmon fisheries off the coasts of Washington, Oregon, and California of the Pacific Fishery Management Council. National Marine Fisheries Service, Northwest and Southwest Regional Fishery Management Divisions. NMFS, 1997. Reinitiated Section 7: Consultation on the fishery management plan for commercial and recreational salmon fisheries off the coasts of Washington, Oregon, and California as it affects the Sacramento River winter chinook salmon. National Marine Fisheries Service, Northwest and Southwest Regional Fishery Management Divisions.

to r_i simply as the "growth rate" of the cohort returning in year i. Denoting the underlying mean growth rate by ρ, the goal of at least a 31% increase in the average cohort replacement rate over the observed mean of 1.35 for the 1989–1993 period is equivalent to a goal, on the log scale, of $\rho_{goal} \geq \log(1.35 \times 1.31) = 0.57$.

A natural recovery benchmark then is to compare the observed sample mean growth rate $\bar{r}$ in future years to ρ_{goal}. If recovery efforts have the desired effect, and if no increased mortality occurs from other causes, recovery will proceed as desired and $\bar{r}$ will likely exceed ρ_{goal}. However, if $\bar{r} < \rho_{goal}$, recovery may not be proceeding as desired and further conservation measures may need to be implemented. This possibility raises the question of how one should evaluate whether an observed $\bar{r} < \rho_{goal}$ warrants concern.

In our paper, we propose using a one-sample, one-sided t-test to evaluate the statistical significance of a difference between the observed mean growth rate and the target rate. We depart from the usual procedure (Lehmann, 1986), however, by conditioning the test on a specific level of statistical power, rather than on a fixed type-I error rate, in order to provide an adequate detection probability for dangerously low population growth rates. Application of the test requires choosing a particular power level and specifying what constitutes a "dangerously" low population growth rate. Together, these quantities determine the sensitivity of the test for detecting population growth rates below the target, and the likelihood of false positives, i.e. concluding that population growth rate is below the target when it in fact is not. The level of danger posed by a certain growth rate is evaluated by using a population viability model.

Figure 1
Map of Northern California depicting the Sacramento River, its upper tributaries, and mainstem dams.

Hypothesis testing and statistical power

Evaluating whether or not winter chinook salmon are meeting the recovery goal requires a statistical test because of the variability inherent in $\bar{r}$. We propose that a one-sided t-test be used to decide whether an observed mean population growth rate falls significantly short of the goal—in which case further regulatory action may be necessary. The null hypothesis of the test is that the underlying mean growth rate ρ (estimated by $\bar{r}$) is greater than or equal to ρ_{goal}, and the alternative hypothesis is that ρ is less than ρ_{goal}. That is,

$$H_0: \rho \geq \rho_{goal}$$

$$H_A: \rho < \rho_{goal}$$

with, in this case, $\rho_{goal} = 0.57$. Given a set of $n > 1$ observed r_i values $\{r_1, r_2, \ldots, r_n\}$, with mean $\bar{r}$ and standard deviation s, the test statistic is

$$\delta = \frac{\rho - \rho_{goal}}{\sigma / \sqrt{n}}, \quad (1)$$

Assuming that the $\{r_i\}$ are independent and identically distributed normal random variables, t has a central t-distribution with $n - 1$ degrees of freedom if $\rho = \rho_{goal}$, and a noncentral t-distribution if $\rho \neq \rho_{goal}$ (Lehmann, 1986). The t-test rejects H_0 in favor of H_A when t is less than some critical value t_c specified *a priori* by the investigator.

A t-test has four possible outcomes, two of which result in correct inference: the test can accept H_0 when it is true, and it can reject H_0 when it is false. The test could also reject H_0 when it is in fact true—a "type-I" error, or it could fail to reject H_0 when it is false—a "type-II" error. The expected rates of type-I and type-II errors are conventionally denoted as α and β, respectively. The probability of correctly rejecting H_0 is known as the power π of the test, and $\pi = 1 - \beta$.

The type-I and type-II error rates are determined by the value of t_c selected for the test. A smaller value of t_c results in a lower type-I error rate α and a higher type-II error rate β. A larger value of t_c has the opposite effects. In all cases, the two error rates change in opposite directions when the value of t_c is changed. Thus, for a given data set of size n, α and β cannot be simultaneously minimized by adjusting t_c.

Given the endangered status of winter chinook salmon, it is clearly necessary to ensure that the statistical test has enough power to detect dangerously low population growth rates. To achieve this goal we propose that the power π of the test be held at a fixed level, rather than the

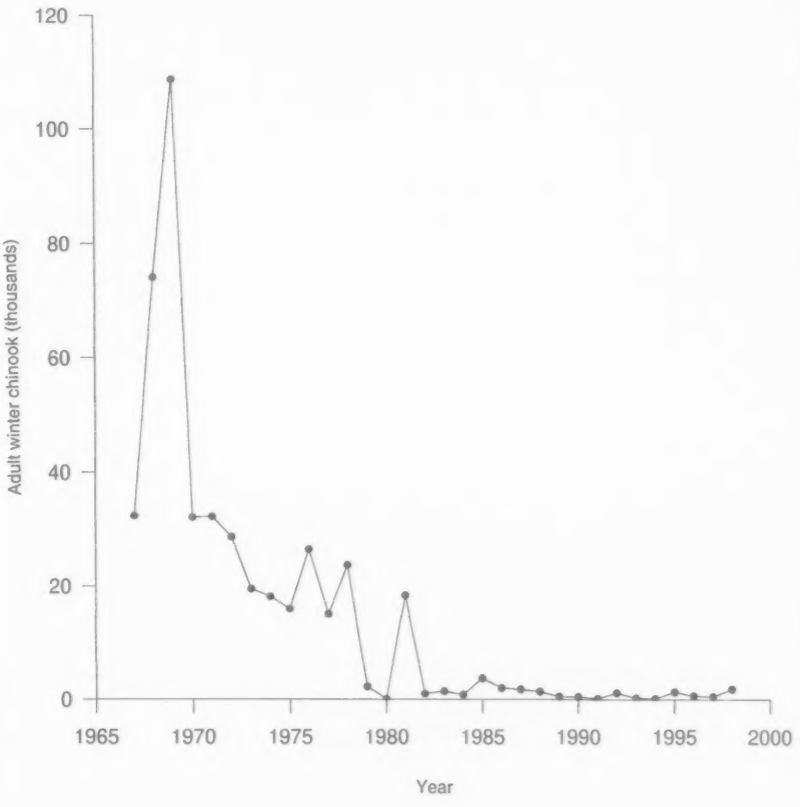

Figure 2
Historical time series of winter chinook salmon adult returns at Red Bluff Diversion Dam.

type-I error rate α. This approach differs from the conventional approach to hypothesis testing in which α is fixed at, say, 0.05, and the resulting power-level is either tolerated, or the sample size n is increased sufficiently to provide an acceptable level of power. Increasing n is not an option in this instance, because in any given year of application the sample size of the $\{r_i\}$ data set will be fixed, and a procedure is required that can be applied in each and every year. In the context of monitoring winter chinook salmon, a failure to reject H_0 may be used to justify "business as usual." By specifying the power π of the test in advance, resource managers will know that if the mean growth rate is falling seriously short of the goal, they will be able to detect this with specified probability π.

Calculation of α given π

In this section, we formulate the relation between π and α. This relation allows one to determine what values of α should be used for the test in order to achieve a specified level of power π.

With the previously stated distributional assumptions, t has a central t-distribution if $\rho = \rho_{goal}$, with cumulative distribution function (cdf) T and inverse cdf T^{-1}. If $\rho \neq \rho_{goal}$, t has a noncentral t-distribution with cdf T_δ, inverse cdf T_δ^{-1}, and noncentrality parameter

$$t = \frac{\bar{r} - \rho_{goal}}{s/\sqrt{n}}. \tag{2}$$

which is the difference between ρ and ρ_{goal} in standard error units (Johnson et al., 1994). Given a particular critical value t_c, the associated type-I error rate and power of the t-test are

$$\alpha = \Pr\{\text{reject } H_0 | H_0 \text{true}\} = T(t_c), \tag{3}$$

$$\pi = \Pr\{\text{reject } H_0 | H_0 \text{false}\} = T_\delta(t_c), \tag{4}$$

α by definition being the largest value of $T_\delta(t_c)$ under H_0, which occurs at $\rho = \rho_{goal}$ where $T_{\delta=0}(t_c) = T(t_c)$. Solving

Equation 4 for t_c and substituting this into Equation 3 gives

$$\alpha = T\left(T_{\delta}^{-1}(\pi)\right). \quad (5)$$

Equation 5 indicates the type-I error rate, α, associated with the test when conducted at specified power-level π. Note that, π having been specified, α also depends on the magnitude of the underlying difference $\rho - \rho_{goal}$, the variability σ in growth rates, and the sample size n, all through the noncentrality parameter δ.

Relation between α, π, n, and quasi-extinction

Although Equation 5 gives the value of α corresponding to a specified power-level π, the formula itself does not reveal the nature of the relation between α and π, and how this relation is affected by ρ and n. We illustrate these relationships below and consider their consequences in the context of a proposed test for detecting low growth rates in the Sacramento River winter chinook salmon population.

To apply Equation 5, we must specify σ, ρ, and π. We want to know (with probability π) that winter chinook salmon growth is not less than ρ_{goal} by a critical amount. Because the ESA is invoked to prevent extinction, we want to guard against growth rates that could lead to extinction. We used the winter chinook salmon population viability model developed by Botsford and Brittnacher (1998) to identify growth rates corresponding to quasi-extinction probabilities of 0.05, 0.50, and 0.99 over 50 years. Quasi-extinction occurs when a population falls below some threshold level, in this case 200 adults in three consecutive cohorts. We initialized the viability model simulation with winter chinook salmon spawning escapements from the 1989–93 base period, and set σ = 0.552, the observed standard deviation of growth rates during the base period, assuming that this value will continue to hold in the future. The mean growth rates corresponding to the specified quasi-extinction probabilities were found to be about 0.0, –0.14, and –0.40, respectively. We note that if indeed $\rho = \rho_{goal} = 0.57$, quasi-extinction is an extremely unlikely event according to this model.

For each of the three growth rates, δ was computed according to Equation 2, and Equation 5 was then used to determine the type-I error rate α over a range of specified power-levels π and sample sizes n. We calculated Equation 5 by using the Matlab Statistics Toolbox function NCTINV (Jones, 1996). (Fortran and S-PLUS subroutines are also available for the noncentral t-distribution from the Carnegie Mellon University Department of Statistics' StatLib and Oxford University Department of Statistics' FTP archive, respectively. Alternatively, because t_{δ} is distributed as a ratio of independent random variables, $(Z+\delta)/\sqrt{\chi^2_{n-1}/(n-1)}$, where Z is a standard normal variate and χ^2_{n-1} is a chi-square variate with $n-1$ degrees of freedom, a large number of draws of t_{δ} could be simulated, and the $100 \times \pi$'th percentile could be taken as an approximation to $T_{\delta}^{-1}(\pi)$ in Equation 5.)

Table 1

Type-I error rate (α) necessary to maintain the t-test power-level at π given a fixed number of observations n. Power-level is with respect to detecting a mean growth rate of ρ.

		n			
ρ	π	2	3	4	5
0.0	0.9	0.435	0.326	0.246	0.185
	0.8	0.308	0.216	0.154	0.110
	0.7	0.238	0.157	0.106	0.073
	0.6	0.188	0.117	0.076	0.050
	0.5	0.148	0.087	0.054	0.034
	0.4	0.114	0.063	0.037	0.023
	0.2	0.054	0.027	0.015	0.008
–0.14	0.9	0.334	0.225	0.152	0.102
	0.8	0.243	0.150	0.094	0.059
	0.7	0.190	0.109	0.065	0.039
	0.6	0.151	0.081	0.046	0.027
	0.5	0.120	0.061	0.033	0.018
	0.4	0.092	0.044	0.023	0.012
	0.2	0.044	0.019	0.009	0.004
–0.40	0.9	0.229	0.125	0.068	0.037
	0.8	0.172	0.084	0.042	0.022
	0.7	0.137	0.062	0.029	0.014
	0.6	0.110	0.046	0.021	0.010
	0.5	0.087	0.035	0.015	0.007
	0.4	0.068	0.025	0.010	0.004
	0.2	0.033	0.011	0.004	0.002

The results for $\rho = 0.0$ (Fig. 3) display the general behavior expected: 1) for fixed π, α decreases with n; 2) for fixed n, the higher π is set, the greater α becomes; and 3) for fixed α, power increases with increased sample size. For example, if the power-level were fixed at $\pi = 0.8$ and α set accordingly, a type-I error would be expected about 22% of the time with 3 years of data, 11% of the time with 5 years of data, or 3% of the time with 10 years of data. On the other hand, if the type-I error rate were fixed at $\alpha = 0.05$, there would be roughly an 80% chance of detecting this value of ρ with 7 years of data, but the power of detection would drop to $\pi < 35\%$ with only 3 years of data.

Table 1 lists results for mean growth rates of 0.0, –0.14 and –0.40. Notice that while the type-I error rate required diminishes for a given power-level and sample size as the underlying growth rate declines, use of a fixed $\alpha = 0.05$ even in the most dire case of $\rho = -0.40$ would provide very low power for $n \leq 3$.

Monitoring protocol

A monitoring protocol cannot be designed solely on the basis of statistical considerations—it must be guided by management policy. In this instance, the management policy is to

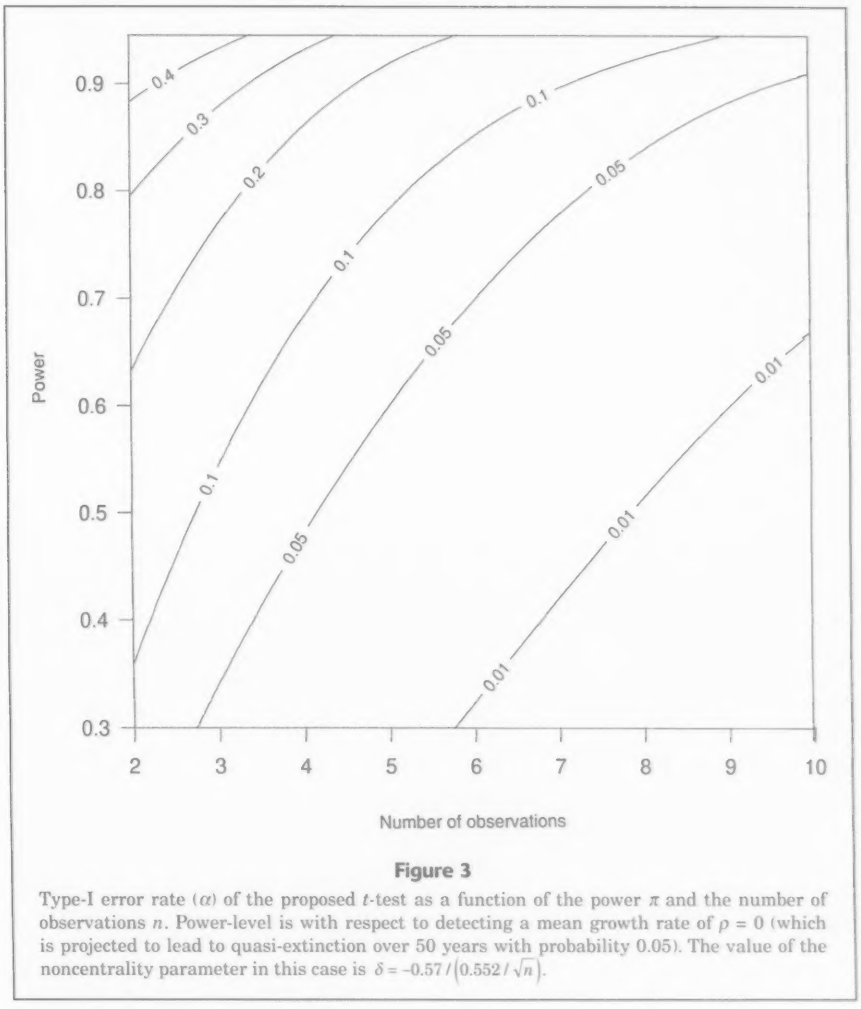

Figure 3

Type-I error rate (α) of the proposed t-test as a function of the power π and the number of observations n. Power-level is with respect to detecting a mean growth rate of $\rho = 0$ (which is projected to lead to quasi-extinction over 50 years with probability 0.05). The value of the noncentrality parameter in this case is $\delta = -0.57 / \left(0.552 / \sqrt{n}\right)$.

provide an adequate level of protection for winter chinook salmon through timely identification of low growth rates, without incurring too many false positive results.

The suggested protocol, therefore, would be to apply the t-test annually, with a fixed power-level of 80% for detecting a mean population growth rate of $\rho = 0$ (which is projected to lead to quasi-extinction over 50 years with probability 0.05). The choice of π and ρ is somewhat arbitrary, reflecting the perceived costs of type-I and type-II errors, and is discussed in a later section of this paper.

The observed growth rates are defined as $r_i = \log(N_i / N_{i-3})$, and the protocol would commence with the $i = 1997$ and 1998 spawning runs—both runs having benefited from the 1996 shift in ocean harvest regulations designed to reduce fishing mortality on winter chinook salmon.[1] Each year after 1998, the additional observed growth rates would be added to the test data set, until five growth rates are obtained. Beyond the year 2001, the test would be limited to the most recent five growth rates, at which point the α-level will stabilize at 0.11. The protocol's moving five-year data frame will facilitate identification of shifts in winter chinook salmon survival and strengthen the basis for the assumption that the $\{r_i\}$ are identically distributed (discussed below). Survival shifts might be expected in response to naturally arising or management-related changes in the freshwater or marine environment.

To illustrate in concrete terms the proposed monitoring and analysis protocol, we applied it to the historical time series of adult returns $i = 1970,\ldots,1996$, as if the protocol had commenced with the $i = 1970$ and 1971 spawning runs. The calculations and results of this application are presented in Table 2. Throughout the historical time series, $\bar{r}$ failed to reach the target level of 0.57, and this failure would have been declared significant in all years except for 1983–89 and 1996. If the test used a higher π, the number of failures declared significant would be higher. For instance, using $\pi = 0.85$ results in 21 null hypothesis

Table 2

Application of the proposed monitoring protocol to the historical time series of winter chinook salmon adult returns at Red Bluff Diversion Dam. Subscript i denotes year; N = abundance; R = cohort replacement rate; r = log (R) = growth rate; $\bar{r}$ = average growth rate over previous n years; t = t-statistic; π = power of test to detect a mean growth rate of zero; α = type-I error rate of test; t_c = test critical value; H_0 = mean growth rate ≥0.57.

Year(i)	N_i	N_{i-3}	R_i	r_i	$\bar{r}_i$	n_i	t_i	π_i	α_i	$t_{c,i}$	Reject $H_{0,i}$?
1967	32321	—	—	—	—	—	—	—	—	—	—
1968	74115	—	—	—	—	—	—	—	—	—	—
1969	108855	—	—	—	—	—	—	—	—	—	—
1970	32085	32321	0.993	–0.007	—	—	—	—	—	—	—
1971	32225	74115	0.435	–0.833	–0.420	2	–2.399	0.8	0.308	–0.689	yes
1972	28592	108855	0.263	–1.337	–0.726	3	–3.343	0.8	0.216	–0.976	yes
1973	19456	32085	0.606	–0.500	–0.669	4	–4.430	0.8	0.154	–1.225	yes
1974	18109	32225	0.562	–0.576	–0.651	5	–5.613	0.8	0.110	–1.453	yes
1975	15932	28592	0.557	–0.585	–0.766	5	–8.718	0.8	0.110	–1.453	yes
1976	26462	19456	1.360	0.308	–0.538	5	–4.252	0.8	0.110	–1.453	yes
1977	15028	18109	0.830	–0.186	–0.308	5	–5.160	0.8	0.110	–1.453	yes
1978	23669	15932	1.486	0.396	–0.129	5	–3.337	0.8	0.110	–1.453	yes
1979	2251	26462	0.085	–2.464	–0.506	5	–2.068	0.8	0.110	–1.453	yes
1980	84	15028	0.006	–5.187	–1.427	5	–1.859	0.8	0.110	–1.453	yes
1981	18297	23669	0.773	–0.257	–1.540	5	–2.041	0.8	0.110	–1.453	yes
1982	972	2251	0.432	–0.840	–1.671	5	–2.243	0.8	0.110	–1.453	yes
1983	1439	84	17.131	2.841	–1.182	5	–1.327	0.8	0.110	–1.453	no
1984	794	18297	0.043	–3.137	–1.316	5	–1.388	0.8	0.110	–1.453	no
1985	3633	972	3.738	1.318	–0.015	5	–0.579	0.8	0.110	–1.453	no
1986	2013	1439	1.399	0.336	0.104	5	–0.462	0.8	0.110	–1.453	no
1987	1761	794	2.218	0.797	0.431	5	–0.141	0.8	0.110	–1.453	no
1988	1386	3633	0.382	–0.964	–0.330	5	–1.129	0.8	0.110	–1.453	no
1989	480	2013	0.238	–1.434	0.011	5	–1.070	0.8	0.110	–1.453	no
1990	425	1761	0.241	–1.422	–0.537	5	–2.386	0.8	0.110	–1.453	yes
1991	134	1386	0.097	–2.336	–1.072	5	–3.173	0.8	0.110	–1.453	yes
1992	1122	480	2.338	0.849	–1.061	5	–3.096	0.8	0.110	–1.453	yes
1993	267	425	0.628	–0.465	–0.961	5	–2.832	0.8	0.110	–1.453	yes
1994	153	134	1.142	0.133	–0.648	5	–2.165	0.8	0.110	–1.453	yes
1995	1296	1122	1.155	0.144	–0.335	5	–1.670	0.8	0.110	–1.453	yes
1996	612	267	2.292	0.829	0.298	5	–1.101	0.8	0.110	–1.453	no

rejections out of 26 tests, rather than the 18 rejections for $\pi = 0.80$. On the other hand, setting $\alpha = 0.05$ would have rejected H_0 only 14 times.

Discussion

Statistical considerations

Any t-test assumes that the observations are independent and are identically distributed normal random variables. Assuming a normal distribution for r is reasonable, because R (its antilog) has been found to be approximately lognormally distributed (Botsford and Brittnacher, 1998). More generally, observations on fish population sizes or survival rates are often found to be approximately lognormally distributed, as if arising from a series of random multiplicative events (Hennemuth, 1980).

The requirement that the growth rate observations be identically distributed as well (same underlying mean and variance), is not directly verifiable, but this assumption is reasonable given the short time period over which the test is conducted (n=5-year period). Indeed, this was our rationale for limiting the testing protocol to a 5-year time horizon. Although a longer time frame would boost the test's sample size and, for fixed α, increase its power, we believe identity of distribution beyond a 5-year horizon is an untenable assumption. Thus, the proposed protocol limits the test to a 5-year time frame, achieving the necessary power at the expense of a higher type-I error rate.

The issue of independence of observations is more difficult to assess. Winter chinook salmon adults return to

the river for spawning at age 3 or age 4, and although approximately 90% of a brood's spawning adults do so at age 3 (Fisher, 1994), this means that there is imperfect temporal isolation between runs in adjacent years. It is plausible that an environmental factor occurring in a particular spawning year could affect the returns in several future years, creating a lack of independence among observations. Such autocorrelation would decrease the effective sample size. Under this scenario, any test based on the nominal sample size (number of years of data) would have increased levels of both type-I and type-II errors (Lehmann, 1986). Given the relatively low level of information available on this population, this consideration is secondary and can be evaluated more thoroughly as the data base increases. The current time series of $\{r_t\}$ values shows no significant autocorrelation ($P>0.05$), which suggests that a lack of independence is most likely not a serious issue.

Choice of δ and π

In any hypothesis test, one must specify the type-I and type-II error rates. The choice of these rates should reflect the relative costs, as perceived by the investigator, of making these errors (Toft and Shea, 1983). When these costs can be specified in advance, and in comparable terms, one can balance them explicitly through specification of α and π (Mapstone, 1995). However, in the case of our proposed winter chinook salmon monitoring protocol, the cost of making a type-I error is unknown (no specific actions have yet been associated with a rejection of the null hypothesis), whereas type-II errors may be associated with extinction. We believe the appropriate course in this situation is to first identify growth rates that lead to unacceptably high probabilities of extinction, fix the power π of detecting these growth rate levels at a suitably high level, and accept, within reasonable limits, the resulting type-I error rate α. Specifically, for the winter chinook salmon monitoring protocol, we have specified an 80% chance of detecting growth rates that would lead to a ≥5% chance of quasi-extinction in 50 years, and accept the corresponding type-I error rate. We have selected these values because they are consistent with suggestions in the literature (reviewed briefly below); resource managers should carefully consider whether they are appropriate.

Setting δ by way of ρ that leads to an unacceptable predicted extinction risk, as we have done, is natural in the current setting, but just what level of extinction risk should be of concern is debatable. Population viability models have been widely used in conservation biology to quantify extinction risk as a function of population size and the magnitude and variability of population growth rate (Beissinger and Westphal [1998] have provided a recent review). Shaffer (1981), in pioneering work on minimum viable populations, has tentatively suggested that viable populations should have at least a 99% chance of remaining extant for 1000 years, but stated that specific probabilities and time horizons are arbitrary, and other values might be more appropriate. Indeed, other studies have used a variety of criteria: Botsford and Brittnacher (1998) used a 0.10 extinction probability in 50 years to develop criteria for removing winter chinook salmon from the Endangered Species List; Shaffer and Samson (1985) used the criteria of a 0.05 extinction probability over 100 years to identify a minimum viable population size for grizzly bears. We have adopted the 0.05 probability of extinction over 50 years as a moderately conservative criterion.

Specifying the value of π is also somewhat arbitrary. Peterman and M'Gonigal (1992) contend that monitoring programs must have high power ($\pi \geq 0.8$) to detect biologically important effects in order to be reliable. A reliable test should also have a reasonable α value as well as sufficient power. In the proposed winter chinook salmon protocol, the α-level stabilizes at 0.11 after 5 years of data have been collected, and we feel that this behavior represents a reasonable balance between the type-I and type-II error rates.

Power analysis and the precautionary approach

With the decline, collapse, or endangerment of numerous fish populations around the world, the paradigm of precautionary fishery management is receiving increasing attention. The "precautionary approach" to fishery management, as developed by the Food and Agriculture Organization of the United Nations (FAO, 1996), strives to avoid irreversible or slowly reversible damage to fisheries, places priority on conservation of productive capacity, and requires that fishing activities be considered harmful unless proven otherwise. The reauthorization of the U. S. Magnuson-Stevens Fishery Conservation and Management Act (as amended through October 11, 1996) is meant to ensure that "irreversible or long-term adverse effects on fishery resources and the marine environment are avoided."

Peterman and M'Gonigal (1992) have argued that power analysis is a fundamental part of precautionary management, because it provides an estimate of the reliability of the monitoring program. There are four types of power analysis, which correspond to determining one of either n, π, α, or the effect size from the other three (Cohen, 1977). In environmental studies, the determination of n and π are fairly common (e.g. Gerrodette, 1987; Gryska et al., 1997; Urquhart et al., 1998). The determination of α, as we have done here, is least common, in part owing to the "strength of the significance criterion convention, which makes investigators loath to consider "large" values of α" (Cohen, 1977).

Type-II errors in fisheries management are costly because populations and ecosystems can be slow to recover (Dayton, 1998). In endangered species management, the biggest risk is extinction of a species, rather than failure to meet some fiscal or harvest goal, and is truly irreversible. Fixing the type-I error rate at a typical value such as 0.01 or 0.05 would make timely detection of dangerously low growth rates unlikely (Table 1; Peterman, 1990). Thus, we believe that using standard statistical protocols, which control for the type-I error rate and accept the resulting type-II error rate, is not an appropriate method when monitoring endangered species. In such situations, it is more logical, and certainly more precautionary, to set the type-II error rate at an acceptably small value that yields a reasonable type-I error rate.

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Seasonal variation in larval fish assemblages in relation to oceanographic conditions in the Abrolhos Bank region off eastern Brazil

Ricardo H. Nonaka
Yasunobu Matsuura
Kazuko Suzuki

Instituto Oceanográfico da Universidade de São Paulo
Cidade Universitária
Butantã, 05508
São Paulo, Brazil
e-mail: nonaka@usp.br

Abstract—The Abrolhos Bank region off the eastern coast of Brazil, under the influence of the Brazil Current, constitutes a typical tropical coral reef ecosystem that is characterized by a high diversity of tropical fish. Results of three ichthyoplankton surveys conducted in this region during summer, autumn, and winter revealed that there were two dominant fish groups: mesopelagic fish and coral-reef-associated fish. From the 45,614 larvae collected, 83 taxa (77 families and 6 orders) were identified, in which the family Myctophidae was the most abundant accounting for more than 25% of the total catch in the three cruises. Among the Myctophidae, seasonal variation in abundance of *Myctophum affine* was significant; there was an outstanding peak in abundance of this species during the summer surveys. The summer peak in abundance of five other species (*Diaphus* spp., *Lepidophanes guentheri, M. nitidulum, M. obtusirostre,* and *Hygophum reinhardtii*) was not as pronounced. Larval distribution patterns of these six species showed no remarkable seasonal change, being evenly distributed over the oceanic area. The coral-reef-associated fish larvae were confined to the bank and adjacent waters. The spatiotemporal distribution patterns of these larvae was strongly influenced by hydrographic features and some seasonal variation was observed. Four larval fish assemblages were identified: Abrolhos Bank, neritic, transitional, and oceanic assemblages. The Abrolhos Bank assemblage was characterized by coral-reef-associated fish, mainly Gobiidae, occupying most areas of the bank on the three cruises. The oceanic assemblage was dominated by mesopelagic fish, especially Myctophidae in all seasons and their occurrence was limited to the open ocean. The transitional assemblage was characterized by a mixture of coral-reef-associated fish and mesopelagic fish, with a seasonal change of dominant groups. It occupied mainly the shelf break area. The small pelagic fish (sardine and anchovy) were the dominant group of the neritic assemblage and occupied the coastal region south of the Abrolhos Bank, where the influence of the South Atlantic Central Water was evident.

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The tropical marine ecosystem is characterized by 1) the presence of coral reefs, which support a large variety of fish communities and benthic fauna that are point sources of eggs and larvae and by 2) the open ocean, where mesopelagic fish dominate the fish community. Thus, the larval fish assemblages in tropical marine ecosystems are a result of the spawning activities of these two communities (Ahlstrom, 1971; 1972; Leis and Goldman, 1987; Flores-Coto and Ordonez-Lopez, 1991; Leis, 1993). The formation of larval fish assemblages is mainly influenced by the reproductive cycles of the adult fish populations. The seasonal cycle of fish spawning activities in the tropics is not pronounced because of a low level of variation in environmental conditions (Lowe-McConnell, 1987).

Distribution patterns of fish larvae in any region of the ocean are related to the reproductive activity of the adult population and to topographic and hydrographic features that affect the dispersal of the larvae. A study of the distribution patterns of fish larvae contributes to an understanding of the interrelationships among fish species during their early life stages, as well as an understanding of adult spawning patterns. In addition, information can be obtained on the reproductive strategies adopted by these fish in response to the physical and biological processes of the region. Distribution patterns among ichthyoplankton species arise from the synchronous reproductive activities of different species that are developed during evolutionary adaptation to geographic and oceanographic conditions. This information is important for a rational use of fishery resources and also for an understanding of the ecological status of the component species in a marine ecosystem.

Ichthyoplankton surveys in Brazilian waters are concentrated off southern Brazil (Matsuura and Olivar, 1999); only a small number of sampling cruises have been conducted off the eastern coast (Aboussousan, 1969; Matsuura, 1985).

In our study, temporal and spatial changes in larval fish assemblages in relation to physical processes of the Abrolhos Bank region were examined. Particular emphasis was placed on the seasonal variation of larval fish assemblages of abundant fish taxa. The objective of the present study is to understand the origin and maintenance of these larval fish assemblages and their relation to oceanographic conditions.

Materials and methods

Three survey cruises were conducted along the eastern coast of Brazil. Two cruises of the FINEP Project (FINanciadora de Estudos e Projetos) were made with the RV *Prof. W. Besnard* in June and November–December of 1978. Sixty-four stations between latitudes 17°S and 23°S were sampled with a Nansen bottle containing a reversing thermometer for hydrographic data and with Bongo nets for collecting zooplankton. The third cruise, that of the JOPS II-9 (Joint Oceanographic ProjectS-II,

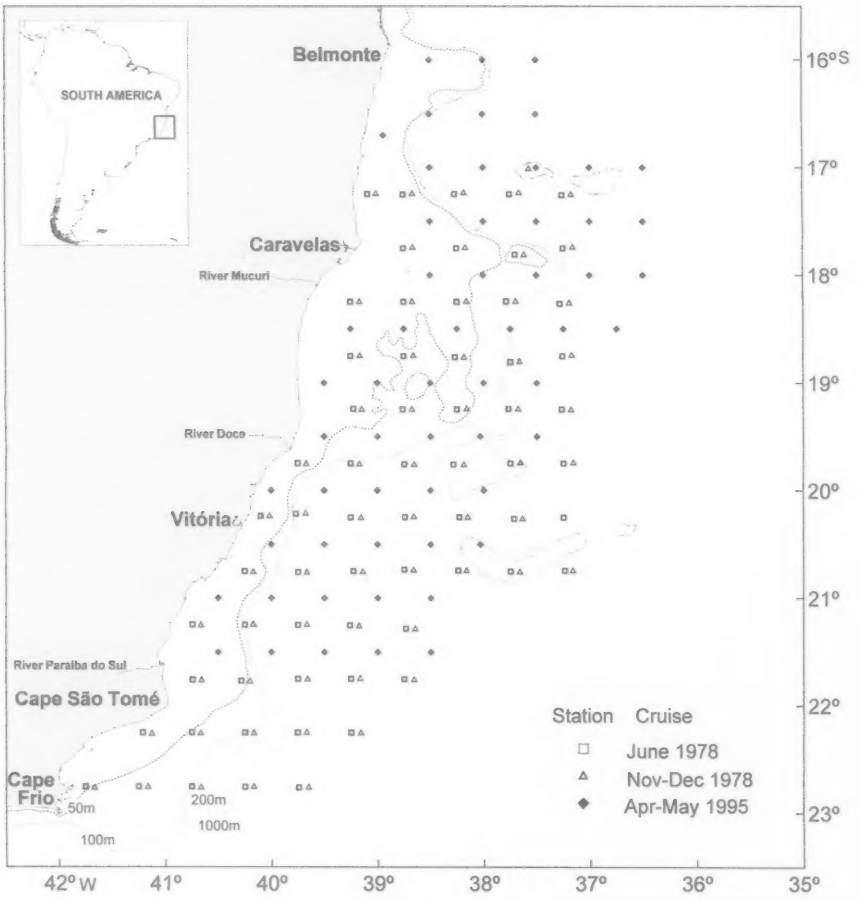

Figure 1

Survey area, sampling stations, and bathymetry off the eastern coast of Brazil.

leg 9), was conducted with the RV *Victor Hensen* in April–May 1995. Fifty-eight stations were sampled between latitudes 16°S and 22°S with a CTD cast for hydrographic data and with Bongo nets for zooplankton (Fig. 1). The interval between stations was 30 nautical miles.

The zooplankton samples were collected by using 60-cm Bongo nets with mesh apertures of 300 µm and 500 µm. The nets were towed obliquely from the surface to a depth of 200 m or down to 5 m above the bottom at shallow stations as the vessel held a 45° wire angle (usually 1.5 knots vessel speed). Winch retrieval rate was 20 m per minute to the surface. In order to increase the water volume filtered, the nets were towed twice down near to the bottom at shallow water (<60 m) stations. The digital flowmeter attached at the center of the net was used to estimate the water volume that was filtered. The plankton samples collected with a 300-µm mesh net were used for both the zooplankton and ichthyoplankton study. Zooplankton volume at each station was measured by using the replacement method (Kramer et al., 1972) and expressed as mL/m^3. The number of fish larvae collected at each station was converted into the number under unit surface area (10 m^2) by using the following equation:

$$Y_i = (10 \times d_i \times x_i) / v_i ,$$

where Y_i = number of standardized larvae under 10 m^2 of sea surface at station i;
x_i = number of larvae taken at station i;
v_i = volume of water filtered (m^3); and
d_i = maximum depth of haul (m).

The total abundance of the larvae of each family was the sum of a standardized number of larvae from all the positive stations. The plankton samples were preserved in a solution of 4% buffered formalin, and the fish eggs and larvae were sorted by using a stereoscopic microscope in the laboratory. Identifications of fish larvae were

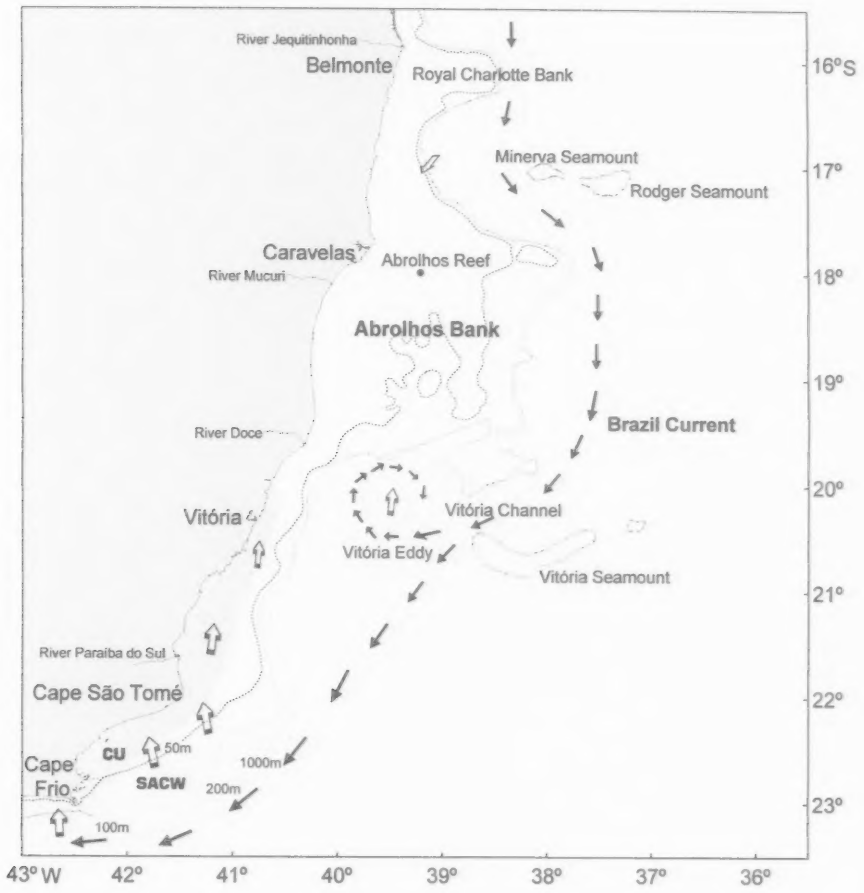

Figure 2

Hydrographic features of the Abrolhos Bank region. The dark arrow shows the main axis of the Brazil Current (BC); the blank arrow the upward movement of the South Atlantic Central Water (SACW), and the shadowed area the coastal upwelling (CU).

based on descriptions in the literature (Fahay, 1983; Leis and Rennis, 1983; Leis and Trnski, 1989; Moser et al., 1984; Moser, 1996; Nafpaktitis et al., 1977; Okiyama, 1988; Olivar, 1988; Olivar and Fortuño, 1991). Larval identification of coral-reef-associated fish is difficult; therefore identification was made only to the family level. The most abundant Myctophidae larvae were identified to species level.

To determine the possible associations among stations, the distribution pattern, and larval abundance, a multivariate analysis of numerical classification was applied by using the two-way indicator species analysis (Hill et al., 1975; Hill, 1979), implemented by the program TWINSPAN. This is a divisive method that classifies stations and families and produces a sorted family by station table, showing the hierarchical classification in binary notation (see "Appendix"). The results of this analysis show the clear ecological preferences of the family groups and are used to identify particular environmental conditions. Only the family groups with an occurrence of more than 10% in each cruise were used in this analysis.

Results

Oceanographic conditions

The continental shelf of the eastern coast of Brazil is generally narrow (ca. 25 km) and is composed of calcareous sediments on the bottom; however, it widens to 230 km offshore at Caravelas (Lat. 18°S), forming the large Abrolhos Bank (AB) to the south (Fig. 2). The depth of shelf break in this region is 100 m with isobathic lines 200 m and 1000 m very close to it. Therefore, we have shown the margin of

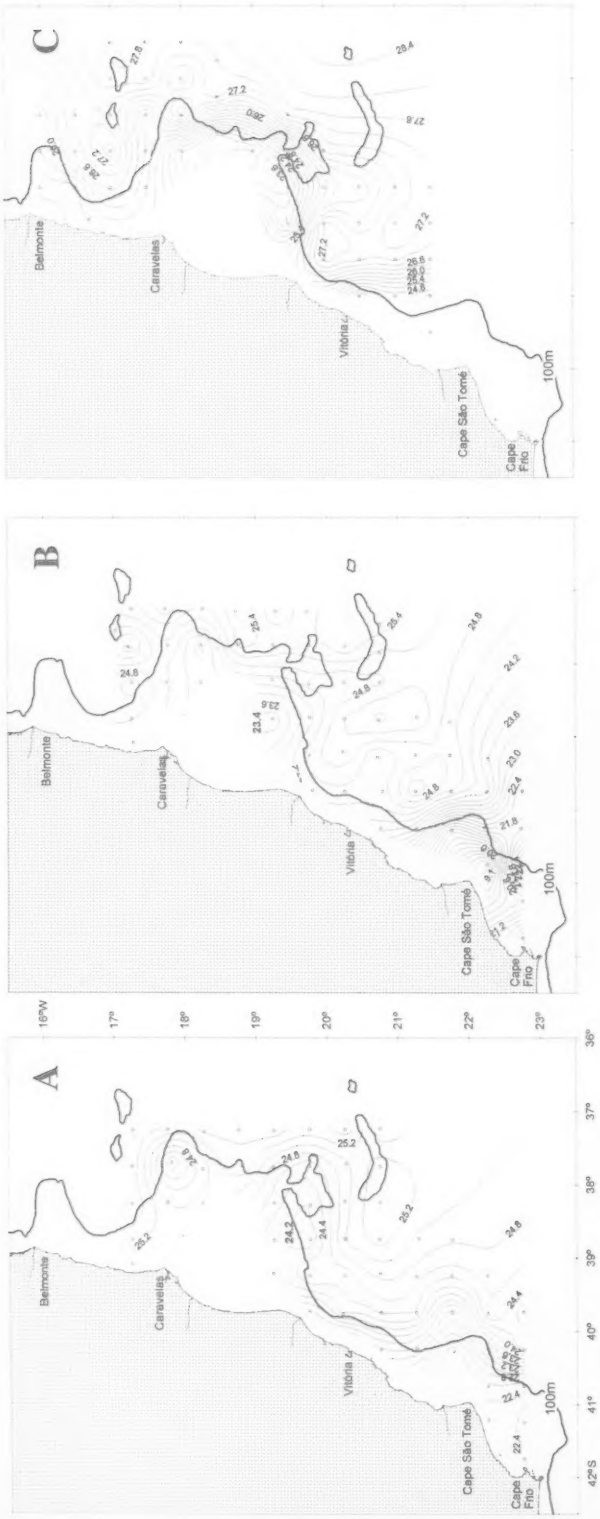

Figure 3

Horizontal distribution of water temperature at 50 m depth for three cruises: winter (**A**); summer (**B**); autumn (**C**) off the eastern coast of Brazil.

continental shelf with the 100-m isobath. This region is characterized by the southward flowing Brazil Current (BC), a typical western boundary current regime (Castro and Miranda, 1998). Because of the topographic impediment of the Abrolhos Bank, the main axis of the Brazil Current flows along the outer edge of the continental slope of the bank and passes through the Vitória Channel formed between the southeastern edge and the Vitória seamount at lat. 20°15′S. It flows southwesterly from this point, approaching the coast near Cape São Tomé (Signorini et al., 1989). Schmid et al. (1995) detected a permanent cyclonic eddy which was formed south of the Abrolhos Bank from the meandering movement of the Brazil Current after passing through the Vitória Channel. Beneath the Brazil Current the South Atlantic Central Water (SACW) occupies the subsurface layer at 120–350 m depth. Prevailing northeast winds induce a coastal upwelling in the region from Cape Frio to Cape São Tomé which is more intense during the austral spring and summer, uplifting the SACW to the surface (Mascarenhas et al., 1971; Silva, 1973; Ikeda et al., 1974).

The horizontal distribution of the water temperature at a depth of 50 m showed a flow pattern similar to that of the Brazil Current on the three cruises, and the thermal front of the SACW of the Cape São Tomé reached the southern rim of the Abrolhos Bank (Fig. 3). The boundary between the Brazil Current and the coastal water was demarcated with a 24.8°C-isotherm line on the three cruises. The temperature gradient between two water masses on the autumn cruise was more pronounced (Fig. 3C). The sea surface temperature at 10 m depth over the Abrolhos Bank ranged from 24.0–25.6°C in winter, and 26.0–26.4°C in summer, to 26.0–28.3°C in autumn. The salinity at 10 m depth ranged from 36.0 to 37.5 psu and showed no seasonal variation.

Zooplankton

The displacement volume of macrozooplankton was low, ranging from 0.07 to1.54 mL/m^3 over the bank and from 0.01 to 0.41 mL/m^3 in the open ocean (Table 1). However, when compared with the displacement volume of macrozooplankton in the north Pacific central gyre, which ranged from 0.05 to 0.10 mL/m^3 (Loeb, 1980), our values in the open ocean were slightly higher.

Table 1
Displacement volume of macrozooplankton (mL/m^3) from three survey cruises in the Abrolhos Bank region.

	Winter		Summer		Autumn	
	Shelf	Open Sea	Shelf	Open Sea	Shelf	Open Sea
No. of stations	26	35	30	34	23	35
Mean volume	0.32	0.09	0.28	0.12	0.26	0.07
Standard deviation	0.219	0.079	0.272	0.047	0.141	0.031
Minimum volume	0.10	0.03	0.07	0.04	0.07	0.01
Maximum volume	1.12	0.41	1.54	0.27	0.69	0.15

Larval fish composition and abundance

A list of the family groups of fish larvae and their abundance is given in Table 2. From the 45,614 larvae collected, 83 taxa (77 families and 6 orders) were identified. The family Myctophidae was the most abundant, accounting for more than 25% of the total catch on the three cruises.

During the winter cruise, 58% of the total larvae taken represented five families in decreasing order of abundance: Myctophidae, Phosichthyidae, Sternoptychidae, Bregmacerotidae, and Serranidae, of which the first four belonged to the mesopelagic fish group.

The total number of larvae collected during the summer cruise was twice as high as that of the other two cruises. Myctophidae represented 27.6% of the total larvae, followed by Scaridae (11.6%), Sternoptychidae (8.2%), Carangidae (4.5%), and Phosichthyidae (4.2%). The following nine families were collected only on the summer cruise: Argentinidae, Clinnidae, Dactyloscopidae, Istiophoridae, Caproidae, Macrorhamphosidae, Malacanthidae, Percophidae and Symphysanodontidae, indicating that these groups spawned only in summer.

During the autumn cruise, the five most abundant families (Myctophidae, Scaridae, Gobiidae, Serranidae, and Phosichthyidae) represented 58.7% of the total larvae taken. Four families (Elopidae, Notosudidae, Scombrolabracidae, and Tripyterigiidae) were collected only in this season, indicating that for these families spawning peaked in autumn.

Seasonal variation in abundance of fish groups

In relation to habitat of adult fish groups, two dominant fish groups were recognized in the survey area: mesopelagic fish and coral-reef-associated fish. Levels of abundance of three families of mesopelagic fish larvae (Myctophidae, Sternoptychidae, and Gonostomatidae) were highest during the summer cruise (Fig. 4). For three other families (Phosichthyidae, Bregmacerotidae, and Paralepididae) levels of abundance were highest for the winter cruise, decreased in summer, and were at a minimum during the autumn cruise. The summer peak in abundance for the myctophid *Myctophum affine* was outstandingly high (Fig. 5). Five other species (*Diaphus* spp., *Lepidophanes guentheri*, *M. nitidulum*, *M. obtusirostre*, and *Hygophum reinhardtii*) were most abundant in summer, but the seasonal differences were not pronounced.

Figure 6 shows a seasonal variation in abundance of the coral-reef-associated fish. Abundance of larval parrotfish (Scaridae) was at a peak in summer, followed by autumn and winter. The same trend was observed in six other families (Labridae, Holocentridae, Balistidae, Pomacanthidae, Acanthuridae, and Pomacentridae). Levels of abundance of larval grouper (Serranidae) were almost the same for three seasons. For the family Gobiidae, a peak in larval abundance was observed during the autumn cruise.

Distribution patterns of fish larvae

Distribution patterns of six species of Myctophidae among each of the cruises are shown in Figure 7. Most of the *Diaphus* spp. larvae were collected at open ocean stations, but also at some coastal stations between Vitória and Cape Frio on the winter and summer cruises. Larvae of *Myctophum affine*, *M. obtusirostre*, *M. nitidulum*, *L. guentheri*, and *H. reinhardtii* were found predominantly at open ocean stations and some at the continental margin, but a considerable number of *Myctophum affine* larvae were also found at coastal stations between Vitória and Cape Frio on the summer cruise (Fig. 7E). The presence of these species along the coast coincided with the presence of the coastal upwelling observed in this area (Fig. 3).

Distribution patterns of the Gobiidae during the summer and autumn cruises were similar, with higher density over the Abrolhos Bank and seamount. Gobiid larvae during the winter cruise were concentrated over the Abrolhos Bank and only a small number of them were collected at open ocean stations south of the bank (Fig. 8). The distribution patterns of the parrotfish larvae (Scaridae) were similar during all three cruises, with higher density at open ocean stations. During the winter cruise the highest densities of grouper larvae (Serranidae) were found around the Vitória Channel, but the Abrolhos Bank stations also showed relatively high density. The stations with the highest densities of grouper larvae during the summer cruise were found along the shelf break and over the seamount. The distribution pattern of grouper larvae during the autumn cruise was different from the former

Table 2

Family groups represented in ichtyoplankton samples collected on the Abrolhos Bank and in adjacent waters off eastern Brazil. Abundance is a sum of a standardized number of larvae from all positive stations and % is a percentage of total abundance.

	Winter Cruise		Summer Cruise		Autumn Cruise	
Taxon	Abundance	%	Abundance	%	Abundance	%
Myctophidae	17911	27.49	31165	27.58	14152	25.44
Scaridae	1224	1.88	13140	11.63	6341	11.40
Sternoptychidae	6042	9.27	9215	8.15	949	1.71
Carangidae	2049	3.14	5103	4.52	544	0.98
Phosichthyidae	6957	10.68	4723	4.18	2380	4.28
Gonostomatidae	414	0.64	4049	3.58	167	0.30
Scombridae	218	0.33	3254	2.88	152	0.27
Engraulidae	1148	1.73	3063	2.71	1075	1.93
Serranidae	3015	4.63	2860	2.53	3704	6.66
Paralepididae	2674	4.10	2527	2.24	672	1.21
Gobiidae	2245	3.45	2280	2.02	6088	10.94
Holocentridae	21	0.03	1976	1.75	54	0.10
Bregmacerotidae	3845	5.90	1657	1.47	1016	1.83
Labridae	114	0.17	1555	1.38	624	1.12
Balistidae	6	0.01	1335	1.18	21	0.04
Pleuronectiformes	625	0.96	1016	0.90	628	1.13
Scorpaenidae	332	0.51	919	0.81	397	0.71
Monacanthidae	94	0.14	857	0.76	353	0.63
Apogonidae	550	0.84	671	0.59	722	1.30
Clupeidae	1248	1.92	660	0.58	483	0.87
Mullidae	1236	1.90	591	0.52	57	0.10
Ophidiiformes	229	0.35	576	0.51	229	0.41
Tetraodontiformes	172	0.26	520	0.46	68	0.12
Pomacentridae	35	0.05	488	0.43	305	0.55
Priacanthidae	0	0	482	0.43	10	0.02
Pomacanthidae	334	0.51	454	0.40	229	0.41
Acanthuridae	44	0.07	424	0.38	127	0.23
Synodontidae	343	0.53	419	0.37	557	1.00
Callionymidae	275	0.42	327	0.29	1872	3.36
Anguilliformes	248	0.38	315	0.28	0	0
Stomiiformes	23	0.03	312	0.28	87	0.16
Triglidae	26	0.04	233	0.21	16	0.03
Gempylidae	110	0.17	210	0.19	84	0.15
Nomeidae	56	0.09	186	0.16	0	0
Lutjanidae	38	0.06	174	0.15	304	0.55
Chaetodontidae	60	0.09	164	0.15	0	0
Cirrhitidae	130	0.20	130	0.12	110	0.20
Exocoetidae	54	0.08	127	0.11	0	0
Syngnathidae	73	0.11	113	0.10	41	0.07
Coryphaenidae	6	0.01	102	0.09	49	0.09
Scopelarchidae	7	0.01	72	0.06	4	0.01
Blenniidae	124	0.19	53	0.05	60	0.11
Chiasmodontidae	42	0.06	50	0.04	75	0.13
Gerreidae	25	0.04	49	0.04	9	0.02
Sphyraenidae	11	0.02	46	0.04	48	0.09

Continued

two and showed an even distribution pattern over the bank and along the shelf break.

The distribution patterns of Clupeidae and Engraulidae were similar; larvae were limited to coastal stations (Fig. 8). The clupeid larvae collected in the coastal region between Vitória and Cape Frio belonged to *Sardinella brasiliensis* and *Harengula jaguana*, and those from the Abrolhos Bank were *Jenkinsia* sp., *Opisthonema* sp., and

Table 2 (continued)

	Winter Cruise		Summer Cruise		Autumn Cruise	
Taxon	Abundance	%	Abundance	%	Abundance	%
Sciaenidae	136	0.21	46	0.04	49	0.09
Fistulariidae	17	0.03	39	0.03	29	0.05
Istiophoridae	0	0	31	0.03	0	0
Lophiiformes	22	0.03	25	0.02	0	0
Percophidae	0	0	22	0.02	0	0
Ostraciidae	0	0	21	0.02	22	0.04
Ogcocephalidae	0	0	20	0.02	6	0.01
Symphysanodontidae	0	0	19	0.02	0	0
Malacanthidae	0	0	18	0.02	0	0
Pomatomidae	11	0.02	18	0.02	2	0
Caproidae	0	0	17	0.02	0	0
Antennariidae	0	0	15	0.01	37	0.07
Carapidae	15	0.02	15	0.01	56	0.10
Echeneidae	0	0	14	0.01	10	0.02
Argentinidae	0	0	13	0.01	0	0
Sparidae	10	0.02	12	0.01	0	0
Trichiuridae	273	0.42	8	0.01	57	0.10
Acropomatidae	153	0.23	6	0.01	400	0.72
Labrisomidae	8	0.01	6	0.01	0	0
Clinnidae	0	0	6	0.005	0	0
Macrorhamphosidae	0	0	4	0.004	0	0
Dactyloscopidae	0	0	4	0.003	0	0
Aulostomidae	9	0.01	3	0.003	99	0.18
Mugilidae	11	0.02	2	0.002	0	0
Opistognathidae	15	0.02	2	0.002	4	0.01
Astronesthidae	7	0.01	0	0	5	0.01
Chlorophthalmidae	33	0.05	0	0	0	0
Elopidae	0	0	0	0	8	0.02
Gadidae	24	0.04	0	0	0	0
Hemiramphidae	12	0.02	0	0	7	0.01
Kyphosidae	6	0.01	0	0	0	0
Melanostomiidae	68	0.10	0	0	15	0.03
Microdesmidae	15	0.02	0	0	10	0.02
Notosudidae	0	0	0	0	31	0.06
Scombrolabracidae	0	0	0	0	4	0.01
Stromateidae	5	0.01	0	0	0	0
Tripyterigiidae	0	0	0	0	4	0.01
Xiphiidae	14	0.02	0	0	6	0.01
Not identified	9856	15.13	13970	12.36	9909	17.81
Total	65154	100.00	112998	100.00	55634	100.00
No. of taxa	65		70		62	

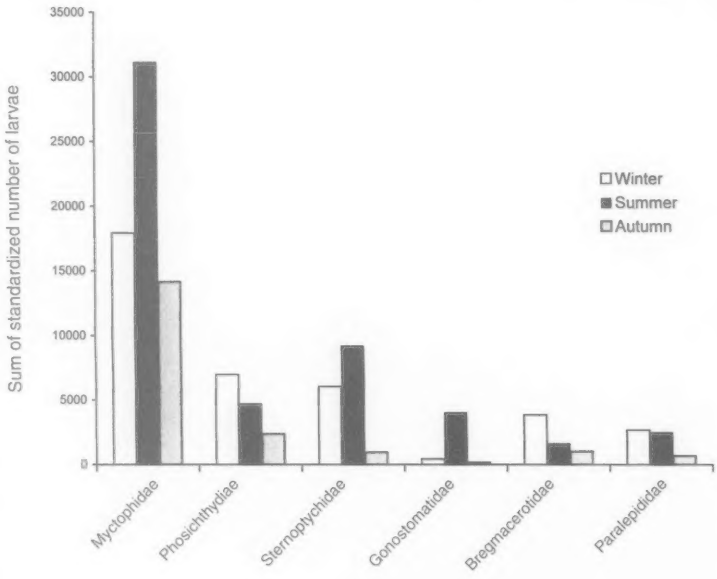

Figure 4

Seasonal variation of larval abundances of mesopelagic fish families in the Abrolhos Bank and adjacent waters.

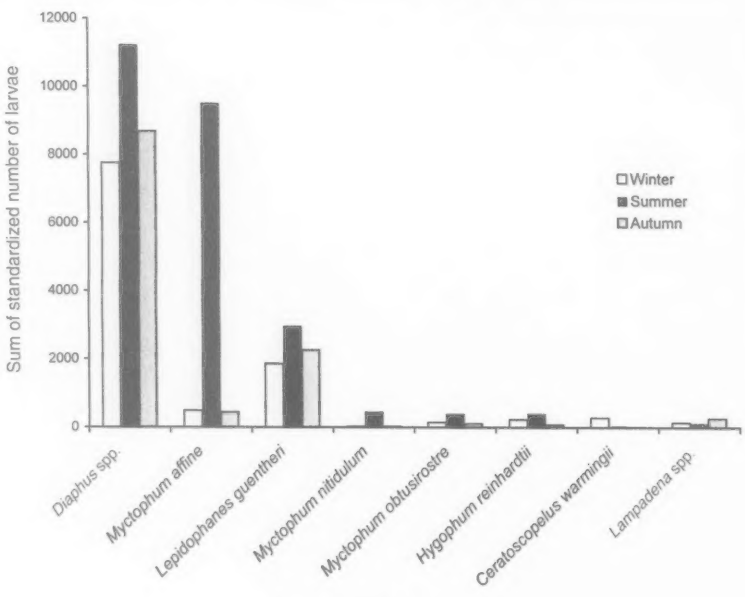

Figure 5

Seasonal variation of larval abundances of lanternfish (Myctophidae) on the Abrolhos Bank and in adjacent waters.

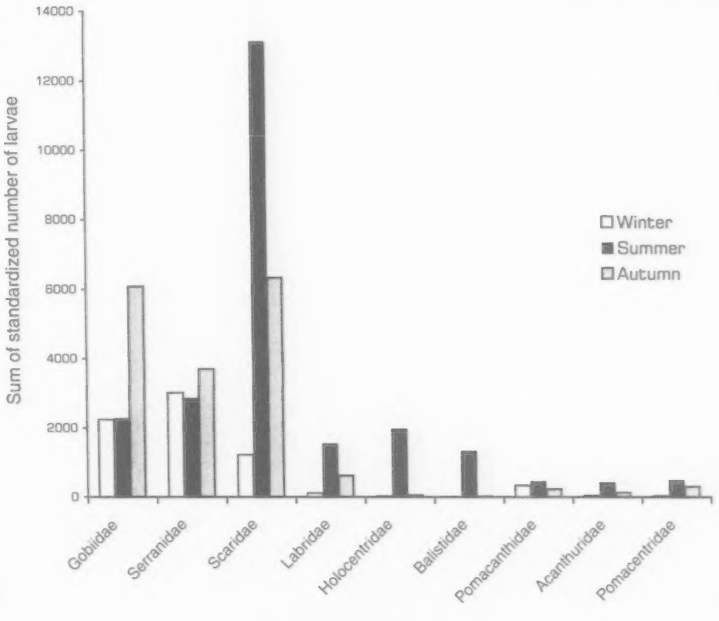

Figure 6
Seasonal variation of larval abundances of coral-reef-associated fish families on the Abrolhos Bank and in adjacent waters

un-identified clupeid larvae. Most of the engraulid larvae collected at coastal stations between Vitória and Cape Frio in winter and autumn were *Engraulis anchoita*, but some larvae found over the AB belonged to *Anchoa* and *Anchovia* that were not identified to species.

Larval fish assemblages

A figure of fish families by station created with the TWINSPAN program is shown in Appendix 1. Clustering the families based on their occurrence and abundance at each station resulted in four major oceanographic groupings: 1) Abrolhos Bank, 2) neritic, 3) transitional, and 4) oceanic.

Abrolhos Bank assemblage The Abrolhos Bank assemblage was situated over the Abrolhos Bank (Fig. 9). During the autumn cruise another subgroup was identified in the coastal region and named "the Abrolhos Bank-coastal assemblage." Taxonomic composition of this assemblage was characterized by the presence of coral-reef-associated fish. The composition was influenced by the seasonal variation of taxa, with the exception of Gobiidae which was the dominant family on all the cruises. The dominant groups of this assemblage were Serranidae, Scaridae, Carangidae, Clupeidae, Apogonidae, Blenniidae, and Labridae.

Neritic assemblage The neritic assemblage was found over the continental shelf between Vitória and Cape Frio. The neritic assemblage was composed of pelagic fish, such as the Clupeidae, Engraulidae, Carangidae, and Bregmacerotidae, as well as the demersal fish Gobiidae and Pleuronectiformes. During the summer cruise the neritic assemblage was limited to the area between Cape São Tomé and Cape Frio, and another subgroup was identified in the northern part between Vitória and Cape São Tomé, named the neritic-north assemblage. This assemblage was characterized by Gobiidae, Engraulidae, and Clupeidae, which accounted for 60% of the total larvae.

Transitional assemblage The transitional assemblage was found mainly along the shelf break area. During the winter cruise the transitional assemblage occurred in two shelf break areas: between Caravelas and Vitória and between Vitória and Cape São Tomé (Fig. 9A). This assemblage was dominated by mesopelagic fish belonging to Myctophidae, Sternoptychidae, Bregmacerotidae, Phosichthyidae, and Paralepididae, but also by the coral-reef-associated fish, such as Serranidae, Carangidae, Mullidae, Pomacanthidae, Apogonidae, and Callionymidae.

The transitional assemblage found during the summer cruise was situated along the outer edge of the Abrolhos Bank, including the oceanic area of the Minerva and Vitória Seamounts (Fig. 9B). Its taxonomic composition was characterized by the great diversity of coral-reef-associated and mesopelagic fish. A transitional-Vitória subassemblage was identified to the south of the Abrol-

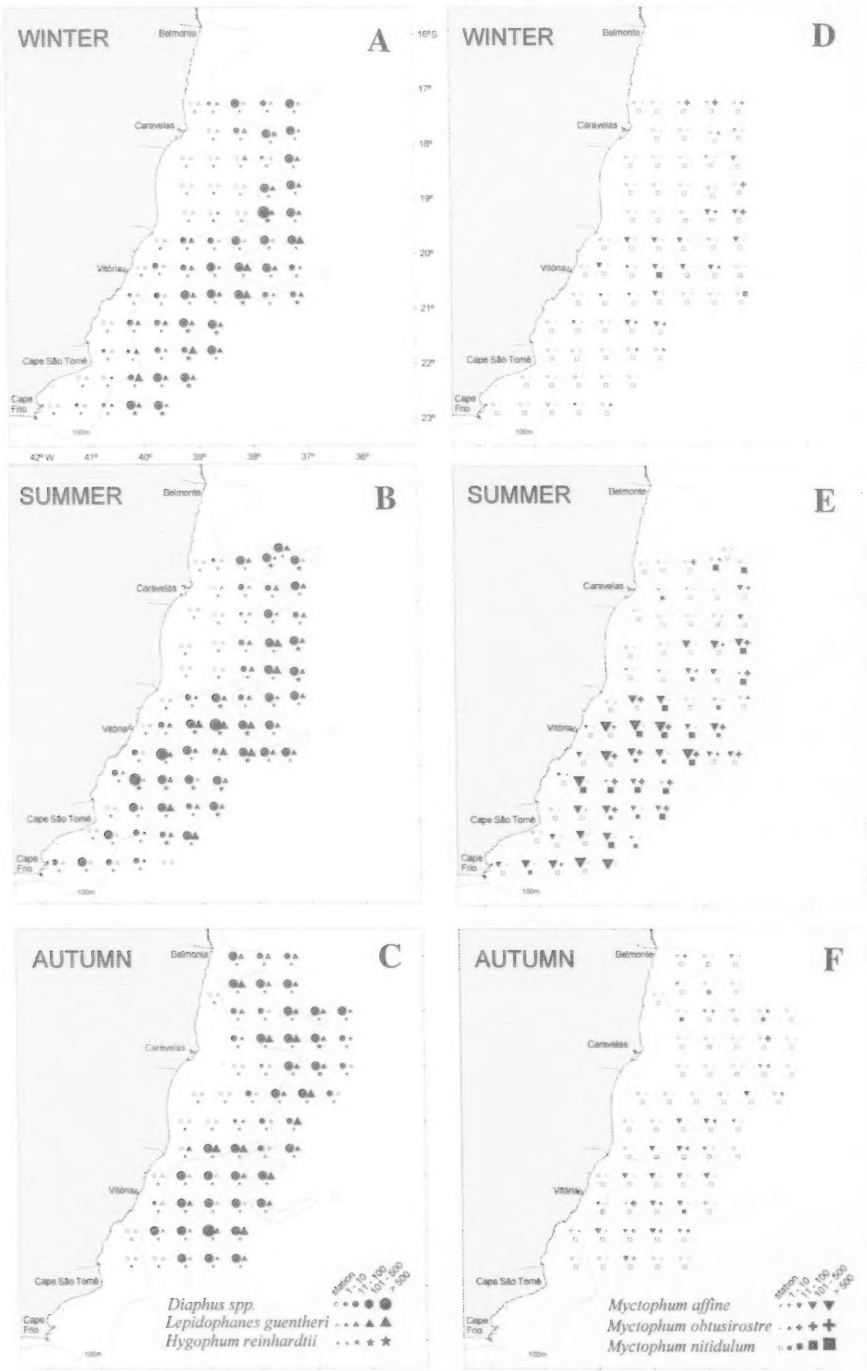

Figure 7

Distribution patterns of lanternfish (Myctophidae) larvae in the Abrolhos Bank region during winter, summer and autumn cruises. (**A–C**): *Lepidophanes guentheri, Hygophum reinhardtii, Diaphus* spp. (**D–F**): *Myctophum affine, M. obtusirostre, M. nitidulum.*

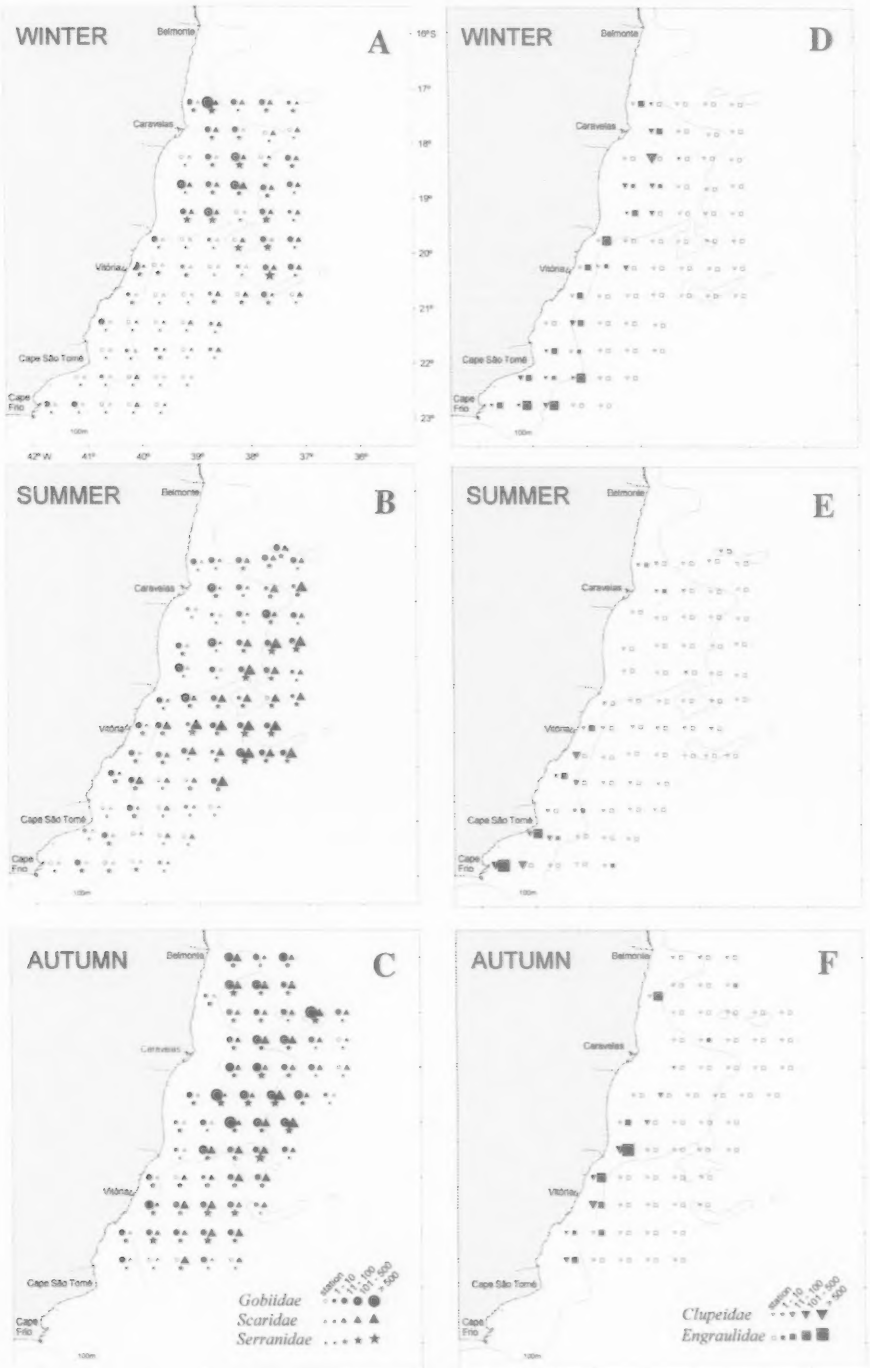

Figure 8

Distribution patterns of coral-reef-associated fish and clupeoid larvae in the Abrolhos Bank region for three cruises: winter (**A, D**), summer (**B, E**) and autumn (**C, F**).

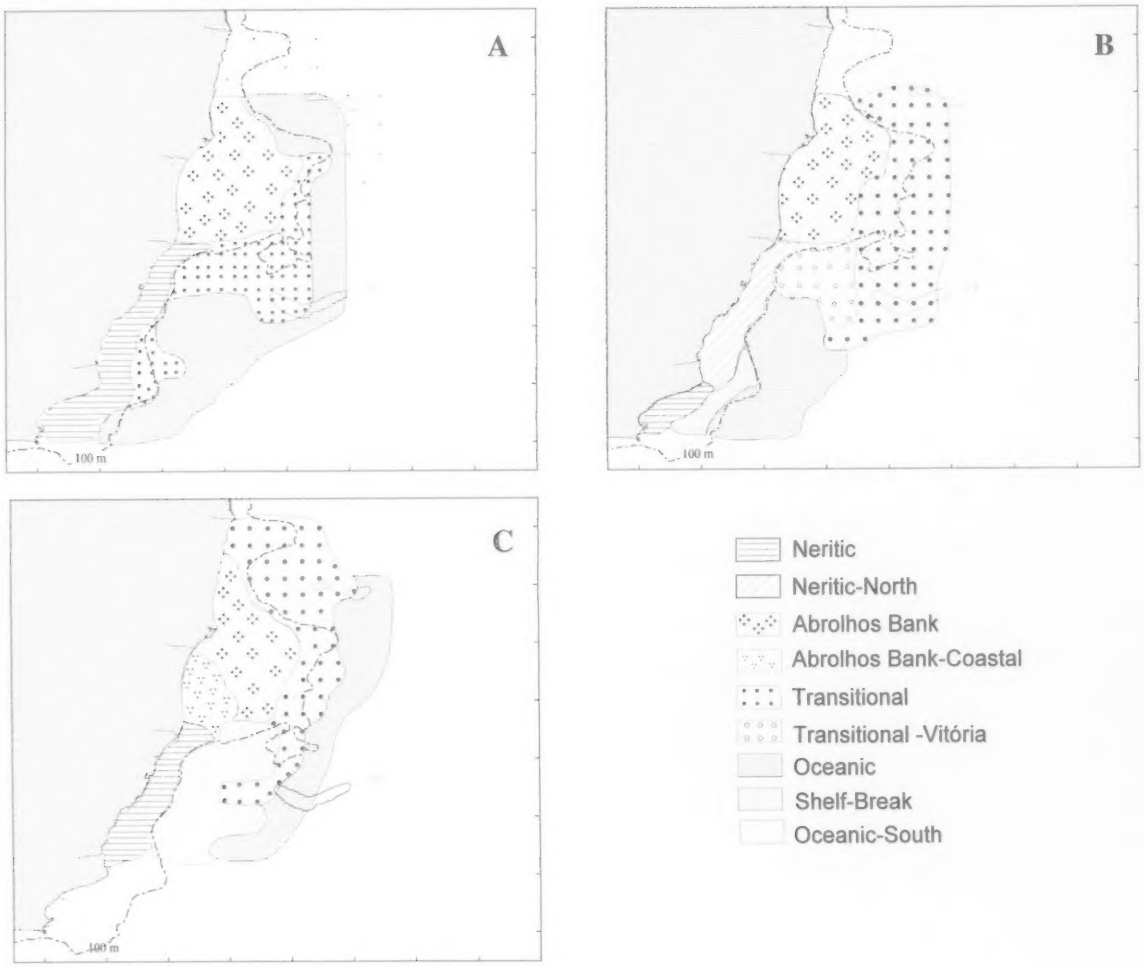

Figure 9

Temporal and spatial distributions of four groups of larval fish assemblages based on the two-way indicator species analysis (TWINSPAN program). (**A**) winter, (**B**) summer and (**C**) autumn.

hos Bank in the oceanic area. The taxonomic composition of this subgroup was similar to that of the transitional assemblage, but mesopelagic fish, such as Myctophidae, Sternoptychidae, and Phosichthyidae dominated.

The transitional assemblage found during the autumn cruise extended along the shelf break area from Royal Charlotte Bank to the Vitória Seamount (Fig. 9C). Its taxonomic composition was predominantly Myctophidae, Scaridae, Gobiidae, Serranidae, Callionymidae, and Apogonidae.

Oceanic assemblage The oceanic assemblage consisted principally of mesopelagic fish (Myctophidae, Phosichthyidae, Sternoptychidae, Paralepididae, and Gonostomatidae). The oceanic assemblage was found in the entire oceanic area from the Minerva Seamount to Cape Frio during the winter cruise. During the summer cruise the same assemblage was limited to the oceanic area between Vitória and Cape Frio. The oceanic subassemblage was detected over the outer continental shelf between River Paraiba do Sul and Cape Frio, named the shelf-break subassemblage. This group was represented by a small number of taxa, predominantly Sternoptychidae. During the autumn cruise the oceanic assemblage was located in the oceanic area from the Roger Seamount to Cape São Tomé and consisted of Myctophidae. The oceanic subassemblage was identified to the south of the Abrolhos Bank, and consisted predominantly of Myctophidae, Phosichthyidae, Scaridae, and Serranidae.

Discussion

The warm and salty tropical water which covers the entire survey area, is transported southward by the Brazil Current. The cold South Atlantic Central Water occupies the subsurface layer beneath the Brazil Current but owing to the deep thermocline (80–120 m), the nutrient rich SACW does not come up to the euphotic zone in the survey area, with exception of the coastal region of Cape Frio-Cape São Tomé. Consequently this area is known to be oligotrophic with a low concentration of nitrates, chlorophyll-*a* biomass, and primary production (Gaeta et al., 1999). The primary production of the nutrient-depleted surface layer is supported principally by autotrophic and heterotrophic picoplankton which use the recycled nutrients in the water. The heterotrophic dinoflagellates and ciliates are responsible for the transfer of energy produced by picoplankton to the upper trophic levels (Susini-Ribeiro,1999).

There was a time gap between the first two cruises (June and November–December in 1978) and the last one (April–May in 1995); therefore the seasonal variations of hydrographic conditions and larval distribution in this region could have been the result of interannual variation. The El Niño year in the tropical Pacific normally causes a drought in the northeastern Brazil and a flood in the south. Bearing in mind that 1978 and 1995 were not atypical El Niño years, we assumed that the interannual variation in hydrographic conditions between these two periods could be ignored. We had no any other information on the interannual variation in oceanographic conditions in this region.

The fish larvae in the Abrolhos Bank region off the eastern coast of Brazil were produced by a diverse collection of fish species that can be divided into two dominant groups: mesopelagic fish and tropical reef fish. The high diversity of taxa (77 families and 6 orders) is characteristic of the tropical marine ecosystem and similar taxonomic diversity of larval fish is known from the eastern tropical Pacific (Ahlstrom, 1971; 1972) and the Gulf of Mexico (Richards et al., 1993).

The most surprising results were the occurrence of many reef-fish larvae along the shelf break areas. Assuming that the reef fish larvae found along the shelf break area off the Abrolhos Bank are transported southward by the main axis of the Brazil Current, most of them should be trapped in the Vitória eddy after passage through the Vitória Channel. Consequently they can be recruited at the southern margin of the bank. In order to prove this hypothesis, an intensive sampling program, coupled with an application of aging technique for postsettlement juveniles, is necessary in this region.

The dominant taxonomic groups (family) from the three cruises showed a distinct seasonal pattern in abundance. The overall larval abundance of the summer cruise was the highest. Among the Myctophidae, the larval abundance of *Myctophum affine* was highest in summer and insignificant in other seasons. Other species (*Diaphus* spp., *Lepidophanes guentheri, Myctophum nitidulum, M. obtusirostre, Hygophum reinhardtii*) also showed relatively high values in summer. Many dominant species concentrate their spawning activities during the austral summer. Myctophid fish in the temperate and subtropical seas are known to spawn mainly from late winter to summer, coinciding with the seasonal peak of zooplankton production in the area (Clarke, 1973; Doyle et al., 1993). The mean displacement volume of macrozooplankton in the open ocean was 33–50% higher in summer than during winter and autumn, suggesting that many fish species have evolved spawning patterns that are synchronized with zooplankton production in this region.

The composition of dominant myctophid larvae in this region is different from that observed on the other side of the South Atlantic, i.e. the *Lampanyctodes hectoris*, a commercially exploited lanternfish, is the most abundant in the Benguela Current, followed by *Symbolophorus* and *Diaphus* (Ahlstrom et al., 1976; Olivar and Shelton, 1993). Meanwhile, the four abundant genera (*Diaphus, Myctophum, Lepidophanes,* and *Hygophum*) in the eastern tropical Pacific (Ahlstrom, 1971; 1972) were also found in the survey area. Most of the *Maurolicus muelleri* larvae were collected from south of Abrolhos Bank in winter and summer, but their occurrence during the autumn cruise was at a minimum. Because the highest densities of *M. muelleri* larvae were recorded in oceanic waters from south Brazil Bight (23–29°S) (Ribeiro, 1996), those found in the survey area may represent only a northern extention of the southern population.

Multivariate analysis of the dominant taxa in the region suggests the existence of geographically distinct larval fish assemblages that show significant seasonal variation. Observed distribution patterns of dominant groups are the result of synchronous and geographically coherent spawning activities of different groups of adult fish. The Abrolhos Bank assemblage was characterized by coral-reef-associated fish, predominantly Gobiidae, on the three cruises. Small pelagic fish were the dominant group in the neritic assemblage. The transitional assemblage was characterized by a mixture of coral-reef-associated fish and mesopelagic fish and a seasonal change of dominant groups. The oceanic assemblage was dominated by the presence of mesopelagic fish, especially the Myctophidae in all seasons.

The general geographic positions of the four larval fish assemblages showed similar distribution patterns on winter and autumn cruises, but those of the summer cruise were slightly different. The oceanic assemblage, which extended in the offshore area from the Minerva Seamount to Cape São Tome in autumn and winter, was limited to the area between Vitória and Cape Frio during the summer cruise. The offshore area between the Minerva and Vitória Seamounts was occupied by the transitional assemblage in summer. The Abrolhos Bank and neritic assemblages consistently occupied most parts of the continental shelf during the three cruises, but different larval fish assemblages occupied the offshore area south of the Abrolhos Bank. This finding can be interpreted as a result of the seasonal variation of hydrographic conditions in this specific area, such as the formation of the Vitória eddy and the intensity of coastal upwelling.

Acknowledgments

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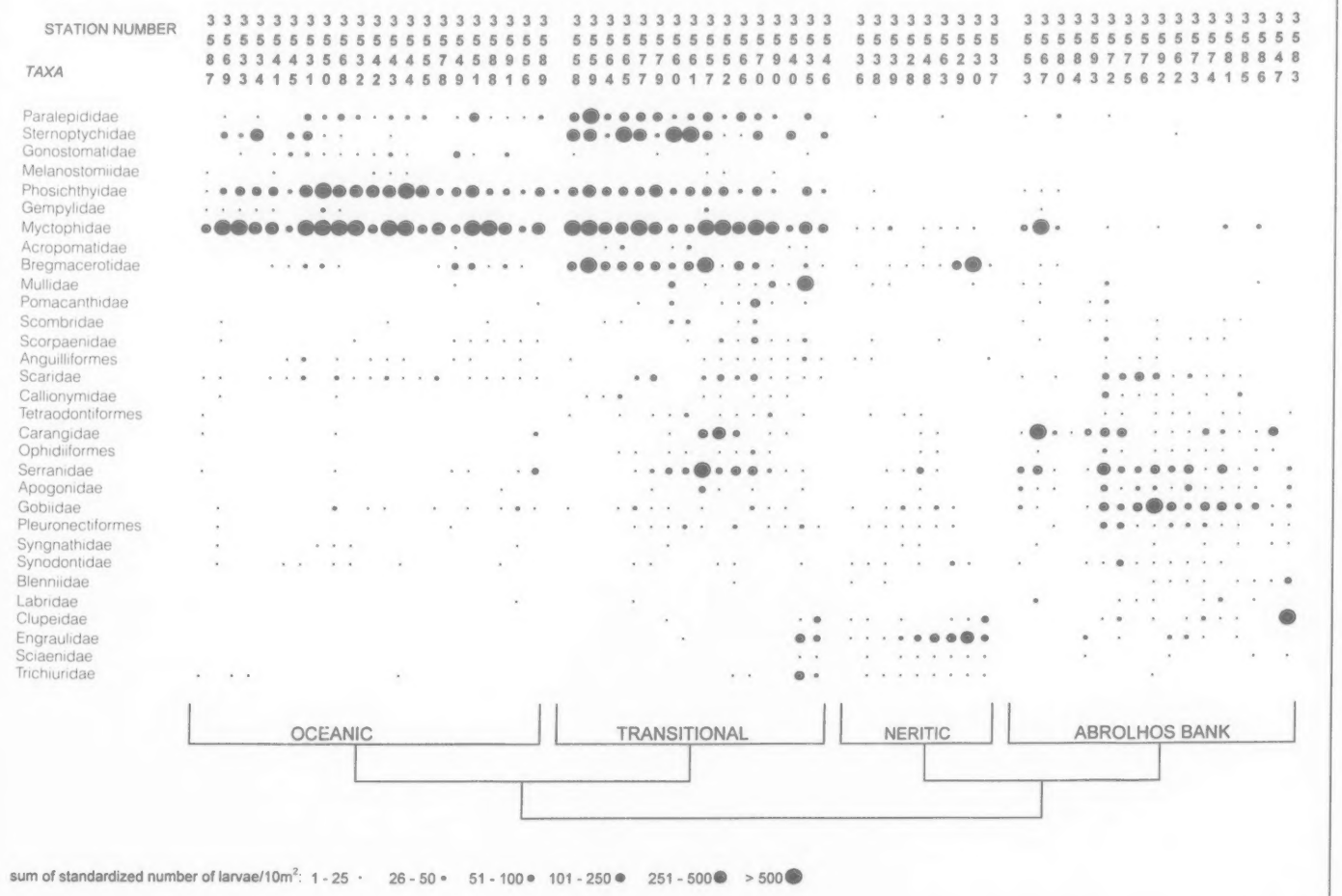
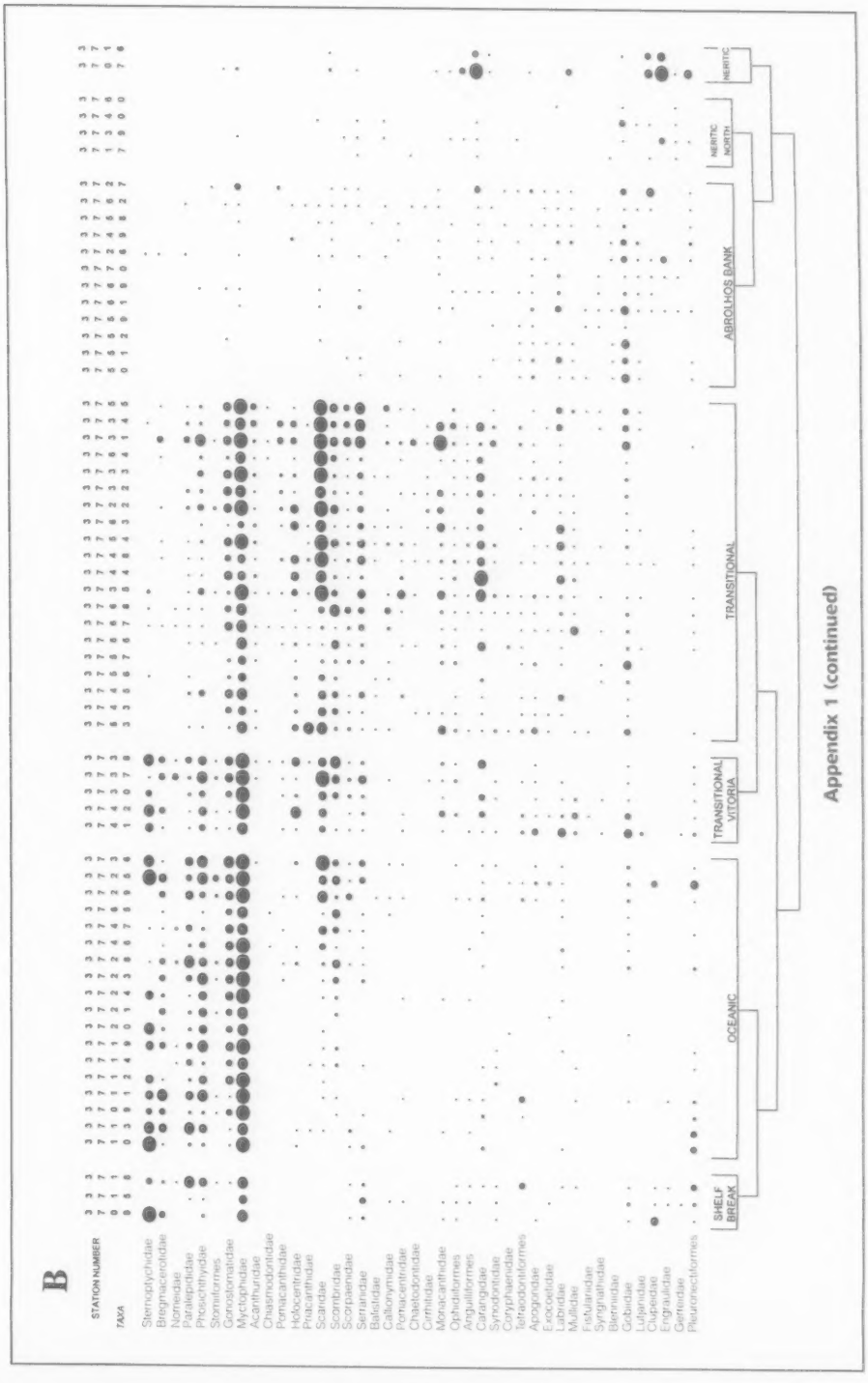
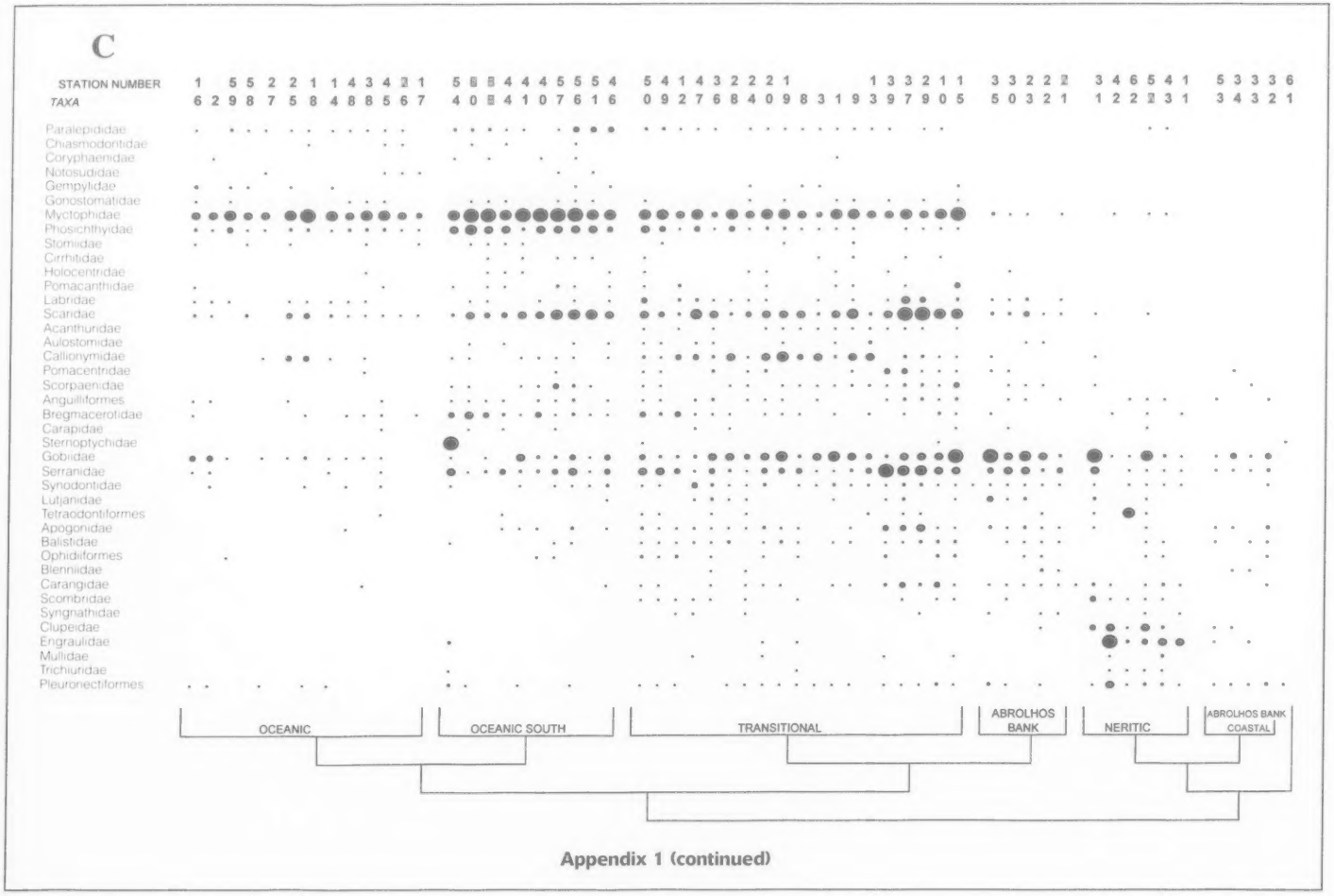


Appendix 1

Figure of stations, with respective families of fish found at these stations, generated by the software program TWINSPAN for the three cruises conducted in the Abrolhos region. Composite clustering of station groups are given along the bottom margin. (**A**) Winter cruise, (**B**) Summer cruise, (**C**) Autumn cruise. TWINSPAN is program CEP-41 in the Cornell Ecology Program series, written by Mark O. Hill.


B
STATION NUMBER
TAXA
Stenoptychidae
Bregmacerotidae
Nomeidae
Paralepididae
Phosichthyidae
Stomiiformes
Gonostomatidae
Myctophidae
Acanthuridae
Chaunacidae
Pomacanthidae
Holocentridae
Pinguipedidae
Scaridae
Scombridae
Scorpaenidae
Serranidae
Balistidae
Callionymidae
Pomacentridae
Chaetodontidae
Cirrhitidae
Moringuidae
Ophidiiformes
Anguilliformes
Carangidae
Synodontidae
Coryphaenidae
Tetraodontiformes
Apogonidae
Exocoetidae
Labridae
Mullidae
Fistularidae
Syngnathidae
Blenniidae
Gobiidae
Lutjanidae
Clupeidae
Engraulidae
Gerreidae
Pleuronectiformes
SHELF BREAK
OCEANIC
TRANSITIONAL VITORIA
TRANSITIONAL
ABROLHOS BANK
NERITIC NORTH
NERITIC
Appendix 1 (continued)



Appendix 1 (continued)

Variation in age compositions and growth rates of *Acanthopagrus butcheri* (Sparidae) among estuaries: some possible contributing factors

Gavin A. Sarre
Ian C. Potter
School of Biological Sciences and Biotechnology
Murdoch University
Western Australia 6150, Australia
E-mail address (for G. A. Sarre): sarre@central.murdoch.edu.au

Abstract—Age compositions and growth rates have been determined for populations of *Acanthopagrus butcheri* in four estuaries and a saline, coastal lake, all of which differ markedly in their morphological, physicochemical, and biotic characteristics. Because the opaque zones in otoliths were shown to form annually, the number of these zones could be used to age individual fish. However, the otoliths of fish that were more than six years old had to be sectioned in order to consistently reveal all opaque zones. The number of annuli on scales did not provide reliable estimates of age. *Acanthopagrus butcheri*, which typically completes its life cycle in estuaries, was represented in each of the five water bodies by fish ≥15 years old and lengths and weights >365 mm and >860 g, respectively. The maximum length and weight of *A. butcheri* recorded in any of the five water bodies were 485 mm and 2196 g, respectively. The values for L_∞ in von Bertalanffy growth equations differed significantly between females and males in three of the four estuarine populations ($P<0.001$ or <0.01), whereas those for both k and t_0 differed significantly between the sexes in only one population and then only at $P < 0.05$. The values for k and L_∞ in the von Bertalanffy growth equations differed significantly among both females and males in the four estuaries at either $P < 0.001$ or $P < 0.05$. These parameters also differed significantly between the males in Lake Clifton and the males in each estuary, except the Swan River Estuary. Growth rates in two of the more northern water bodies were greater than those in the two southern and cooler estuaries. The pattern of growth in the Moore River Estuary, as reflected by changes in length with time, differed from that in the other four water bodies in that it was initially slower and subsequently did not show such a marked tendency to form an asymptote. The slow initial rate of increase in length in the Moore River Estuary may be related to particularly high densities of juvenile *A. butcheri* in nearshore, shallow water, as well as to a relatively lower abundance of appropriate food or very low salinities, or to both of the latter. The percentage contribution made by fish ≥5 years was the lowest by far in the Swan River Estuary, which was subjected to the greatest fishing pressure.

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The black bream, *Acanthopagrus butcheri*, which completes its life cycle within estuaries (Potter and Hyndes, 1999; Sarre and Potter, 1999) is one of the most important recreational and commercial fish species in the estuaries of southern Australia (Lenanton and Potter, 1987; Kailola et al., 1993). The fact that the genetic compositions of the populations of this species in the different estuaries of southwestern Australia vary, suggests that, although some *A. butcheri* are occasionally flushed out of estuaries during those winters when freshwater discharge is particularly heavy, the population in an estuary remains essentially discrete from those in other estuaries (Chaplin et al., 1998; Potter and Hyndes, 1999). The confinement of each population of *A. butcheri* to its natal environment means that, if fishing pressure is sufficiently high in any one estuary, the population in that estuary cannot be replenished naturally by immigration from outside that system. Indeed, there is good evidence that the abundance of this sparid in the Blackwood River Estuary in southwestern Australia declined markedly between the 1970s and 1990s as a result of a combination of commercial and recreational fishing activities (see Valesini et al., 1997; Lenanton et al., 1999; Lenanton[1]; Valesini[2]).

The increasing potential for *A. butcheri* to become overexploited as recreational fishing in estuaries increases means that it is now important to have information on the age compositions of this species in the various estuaries in order to ascertain whether the older age classes are becoming excessively depleted in some of these estuaries. Such data are dependent on accurate estimates of the age of fish. In the past, such estimates for *A. butcheri* have typically been based on the number of annuli on scales (Butcher, 1945; Thomson, 1957; Weng, 1971; Hobday and Moran[3]). However, no attempt was made in any of these studies to use traditional methods to validate that the growth zones (annuli) on that hard structure are formed annually—a procedure now considered essential in aging fish (Beamish and McFarlane, 1983). Although Morison et al. (1998) have recently used the number of opaque zones on otoliths as a criterion of age, their approach to validating that those zones were formed annually was based on the observation that the number of opaque zones on the otoliths of fish in the two cohorts that were the most strongly represented in length-frequency data for four consecutive years increased by one in each successive year.

Recent work on *A. butcheri* in southwestern Australia has focused on populations in four estuaries and a landlocked saline, coastal lake, which vary

[1] Lenanton, R. C. J. 1977. Aspects of the ecology of fish and commercial crustaceans of the Blackwood River Estuary, Western Australia. Report 19, Department of Fisheries and Wildlife, Perth, Western Australia, Australia, 72 p.

[2] Valesini, F. J. 1995. Characteristics of the ichthyofaunas of the Blackwood River Estuary and Flinders Bay. Unpublished honours thesis, Murdoch University, Perth, Western Australia, Australia, 67 p.

[3] Hobday, D., and Moran, M. 1983. Age, growth and fluctuating year class strength of black bream in the Gippsland Lakes, Victoria. Report No. 20. Marine Science Laboratories, Victoria, Australia, 17 p.

markedly in their morphological and physicochemical characteristics and in the composition of their biota (Sarre et al., 2000). Thus, two of these water bodies are permanently open to the sea, while one is intermittently closed, another is normally closed, and one is permanently closed. Furthermore, the regions where *A. butcheri* spawns in these estuaries in the spring and early autumn range in salinity from as low as 3.5–8.0‰ in the intermittently open estuary to over 40‰ in the normally closed estuary and, as a result of their location at different latitudes, they also differ in water temperature (Young et al., 1997; Sarre and Potter, 1999). The differences in the biota of these systems are reflected in marked differences in the dietary composition of *A. butcheri*, with, for example, the overall contribution made by macrophytes to the volume of stomach contents ranging from as low as 8.3% in one population to as high as 56.4% in another (Sarre et al., 2000).

The aims of our study on *A. butcheri* were as follows: 1) to validate that the growth (opaque) zones visible on sectioned otoliths of *A. butcheri* are formed annually; 2) to compare the number of growth (opaque) zones in otoliths prior to and after sectioning in order to determine whether otoliths always have to be sectioned to reveal each of their opaque zones; 3) to ascertain whether the number of annuli on scales corresponds to the number of opaque zones on sectioned otoliths and can thus likewise be used for aging this species; 4) to determine the age composition of *A. butcheri* in the above four estuaries and the saline, coastal lake, in which the fishing pressure on black bream varies from zero to substantial, and thereby ascertain whether there is evidence that heavy exploitation of this species can markedly reduce the proportion of older fish; and 5) to determine the extent to which the growth rates and length at age of *A. butcheri* differ amongst populations in the above five water bodies, which vary markedly in their abiotic and biotic characteristics and amongst which the dietary compositions of *A. butcheri* are significantly different.

Materials and methods

Acanthopagrus butcheri was collected from the permanently open Swan River and intermittently open Moore River estuaries on the lower west coast of Australia (31–32°S) and from the permanently open Nornalup Walpole and normally closed Wellstead estuaries (34–35°S) on the southern coast of Western Australia (see Fig. 1 for locations of these estuaries). *Acanthopagrus butcheri* was also collected from Lake Clifton, a landlocked saline, coastal lake. Because the Department of Conservation and Land Management (CALM) restricted the number of *A. butcheri* that could be collected from this lake to 100, and because 85 of these 100 fish were males, emphasis was placed on the data obtained for this sex in this lacustrine environment.

Fish in estuaries were collected from over sand in nearshore, shallow waters (<1.5 m depth) by using a 41-m seine net with 9-mm mesh in the codend and from offshore, deeper waters (2–5 m depth) by employing composite sunken gill nets containing eight 20 m long × 2 m high panels, each of which had a different mesh size, i.e. 38, 51, 63, 76, 89, 102, 115, or 127 mm. Sampling in the Swan River Estuary commenced in September 1993 and was carried out monthly until April 1995 with seine netting and monthly until February 1995 with gill netting. The same methods were used to sample *A. butcheri* in the Moore River, Nornalup Walpole, and Wellstead estuaries between the spring of 1993 and the summer of 1996–97 (December–January). Sampling in the Swan River, Nornalup Walpole, and Wellstead estuaries was carried out in the saline lower reaches of the tributary rivers, i.e. upper estuary (Fig. 1), which, for most of the year, contain the majority of the *A. butcheri* found in those estuaries (Sarre and Potter, 1999). In contrast, sampling was undertaken throughout the short Moore River Estuary, which does not possess the large central basins that are found in the other three estuaries (Fig. 1). The catches obtained by seine and gill netting in the above four estuaries were supplemented by up to a further 7% by fish obtained with rod and line. A fine mesh seine net, which was 5.5 m long and consisted of 1-mm mesh, was used to collect small *A. butcheri* from extensive beds of the macroalgae *Gracilaria verrucosa* in the downstream and middle regions of the upper Swan River Estuary between December 1998 and March 1999. (See "Results" section for the reason for this additional sampling). The sample of 100 *A. butcheri* collected from Lake Clifton in November 1996 was obtained exclusively by rod and line, in accordance with the conditions laid down by CALM.

Both of the sagittal otoliths were removed from each fish sampled from the four estuaries and Lake Clifton and these otoliths were immersed in methyl salicylate solution. For sectioning, otoliths were mounted and embedded in clear epoxy resin and cut into ca 0.5-mm transverse sections with an Isomet low-speed diamond saw. Sections were ground on sequentially finer grades of carborundum paper (400–1200 grade) and mounted on glass slides with DePX mounting adhesive. Whole otoliths and sectioned otoliths were placed on a black surface and examined microscopically under reflected light.

Measurements were made of the distance between the outer edge of the outermost opaque zone and the periphery of the otolith in the case of the otoliths that were to be used for aging fish in the Swan River Estuary. This distance, i.e. the marginal increment, was then expressed either as a proportion of the distance between the primordium of the otolith and the outer edge of the opaque zone, when only one opaque zone was present, or as a proportion of the distance between the outer edge of the two outermost opaque zones, when two or more opaque zones were present. All measurements were recorded to the nearest 0.05 mm. As with other sparids, a narrow opaque zone is laid down in the otoliths of *A. butcheri* during the cool (winter) period and a wide translucent zone is deposited during the warm (summer) period (Johnson, 1983; Buxton and Clarke, 1991; Francis et al., 1992; Booth and Buxton, 1997).

Otoliths from 239 *A. butcheri*, collected from the Swan River Estuary and covering a wide size range, were used for comparing the number of narrow, opaque zones that could be seen on this hard structure before and after sectioning. The number of opaque zones visible in a subsam-

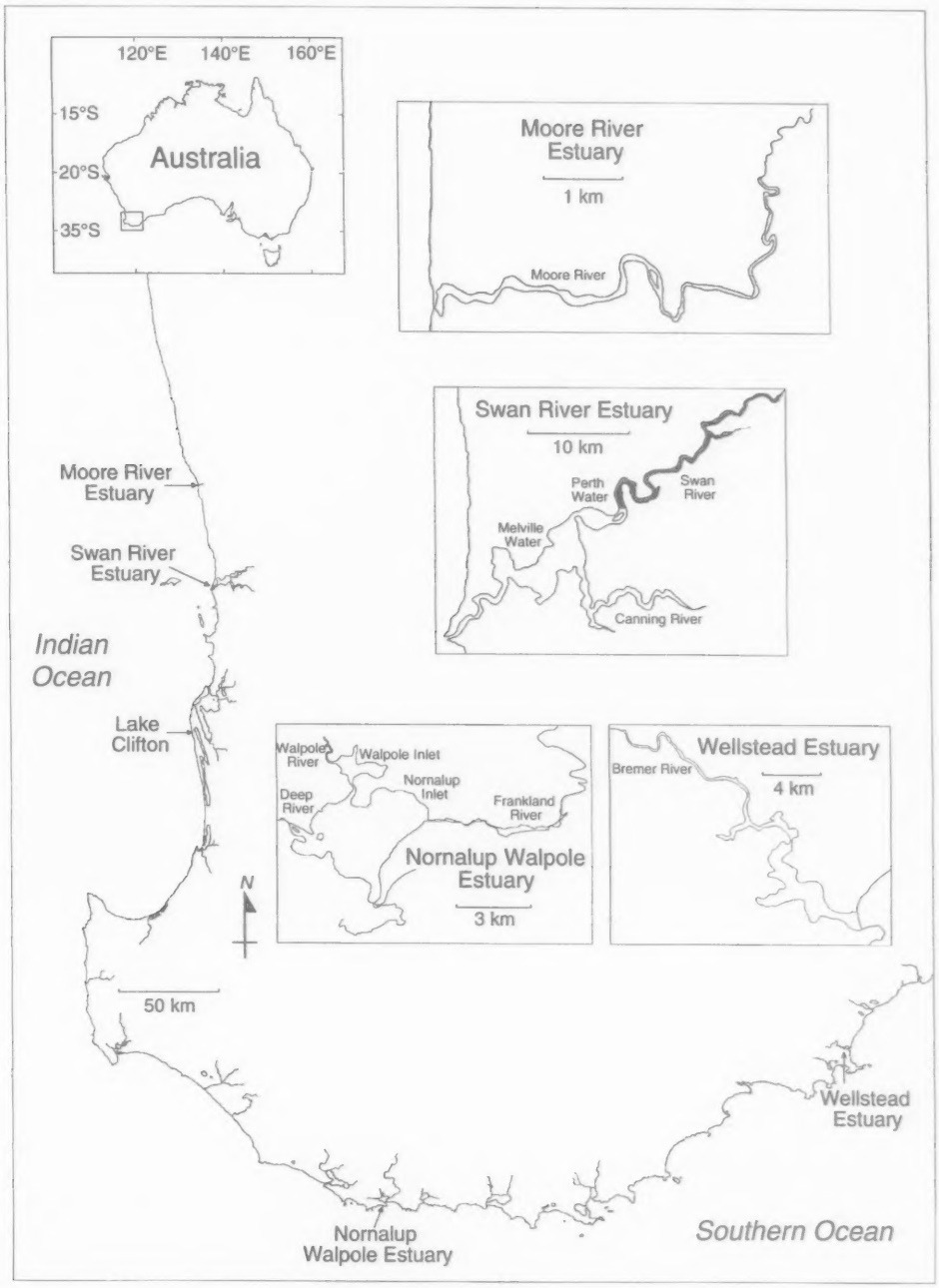

Figure 1

Map showing the location of the four estuaries and Lake Clifton in southwestern Australia from which samples of *Acanthopagrus butcheri* were collected, together with individual maps of each estuary. The shaded area of the Swan River Estuary represents the region sampled in our study.

ple of 126 of the sectioned otoliths were then compared with the numbers of annuli on scales removed from the same fish. The scales used for these comparisons, which were obtained from above the lateral line and directly behind the operculum, were mounted between glass slides and examined microscopically under reflected light.

The number of opaque zones in the whole and sectioned otoliths of a subsample of 162 of the above 239 fish and the number of annuli on the scales of a random subsample of 87 of those fish were also counted by a second reader to determine the level of reproducibility of the counts made of the growth zones on these hard structures by the senior author.

The birth date assigned to *A. butcheri* in each water body corresponds to peak spawning activity, as estimated from the trends exhibited by gonadosomatic indices, stages in gonadal development and pattern of oocyte development (Sarre and Potter, 1999). Von Bertalanffy growth curves were fitted to the individual lengths of female and male fish at their estimated ages at capture by a nonlinear technique (Gallucci and Quinn, 1979) by using a nonlinear subroutine in SPSS (SPSS Inc., 1988). The von Bertalanffy equation is

$$L_t = L_\infty\left[1-e^{-k(t-t_0)}\right],$$

where L_t = the total length at age t (years);
L_∞ = the mean of the asymptote predicted by the equation;
k = the growth coefficient; and
t_0 = the hypothetical age at which fish would have zero length, if growth followed that predicted by the equation.

The lengths at age of fish whose sex could not be determined under a dissecting microscope were selected at random and placed alternately in the data sets for female and male fish.

Each of the growth parameter estimates for female and male fish in the same estuary and for each sex in the four estuaries were compared by using a likelihood ratio test (see Kimura, 1980). Comparisons were also made between the growth parameters for the males of *A. butcheri* in Lake Clifton, the sex which dominated the catches in that lake, and those of the males of this species in the four estuaries.

The likelihood ratio for the null hypothesis (Kimura, 1980) tests the null hypothesis against the alternative hypothesis where

H_ω states that the parameters L_∞, k ,and t_0 satisfy some set of r linear constraints;

H_Ω states that the parameters L_∞, k, and t_0 possibly satisfy no linear constraints.

The maximum likelihood estimates of the error variances $\hat{\sigma}^2_\omega$ and $\hat{\sigma}^2_\Omega(r)$ are given by the sum of squares of residuals from the iteratively reweighted least squares procedure used to fit L_∞, k, and t_0 subject to r linear constraints.

The likelihood ratio test statistic, as described by Cerrato (1990), for two data sets with sample sizes n_1 and n_2 is given by

$$-2\log(\Lambda),$$

where $$\Lambda = \left(\frac{\hat{\sigma}^2_{1\omega}}{\hat{\sigma}^2_{1\Omega}}\right)^{n_1/2}\left(\frac{\hat{\sigma}^2_{2\omega}}{\hat{\sigma}^2_{2\Omega}}\right)^{n_2/2}.$$

Table 1

The linear constraints and degrees of freedom of each hypothesis, based on Kimura (1980), where $_M$ and $_F$ represent males and females, respectively.

Hypothesis	Linear constraints	Degrees of freedom
H_Ω	none	
$H_{\omega 1}$	$L_{\infty M} = L_{\infty F}$	1
$H_{\omega 2}$	$k_M = k_F$	1
$H_{\omega\beta}$	$t_{0M} = t_{0F}$	1

Under the null hypothesis $-2\log(\Lambda)$ converges to a $\chi^2(r)$ distribution with the degrees of freedom equal to the number of equations required to specify the linear constraints applied to the model (Kimura, 1980). The null hypothesis is rejected at the α level of significance when $-2\log(\Lambda) > \chi^2(r)$.

The types of linear constraints applied to the von Bertalanffy growth equation, the null and alternative hypotheses associated with each constraint and the degrees of freedom of the test statistic are given in Table 1.

Results

Validation of annual deposition of opaque zones in otoliths

The mean monthly marginal increment on sectioned otoliths with one opaque zone declined sharply from 0.57 in September and October 1993 to 0.11 in November 1993, before gradually rising to a maximum of 0.93 in October 1994 (Fig. 2). As in 1993, the mean marginal increment then declined markedly between October and November 1994 and subsequently rose over the ensuing months. The trends exhibited by the mean monthly marginal increment on otoliths with two and three opaque zones were the same as those just described for otoliths with one opaque zone (Fig. 2). Because the number of fish with otoliths displaying four or more opaque zones in the samples for some months was small, the marginal increments for all such otoliths in each month were pooled. Although the trends shown by the mean monthly marginal increments on these otoliths were not quite as "smooth" as those shown by otoliths with one to three opaque zones, they still clearly declined precipitously in November of both 1993 and 1994 and subsequently rose progressively during the ensuing months between early summer and mid-autumn (Fig. 2).

The fact that, irrespective of the number of opaque zones on otoliths, the mean monthly marginal increments on otoliths underwent a pronounced decline and then a progressive rise only once during the year demonstrates that a single opaque zone is formed in otoliths each year. Thus, the number of opaque zones in sectioned otoliths can be used to determine the age of *A. butcheri*.

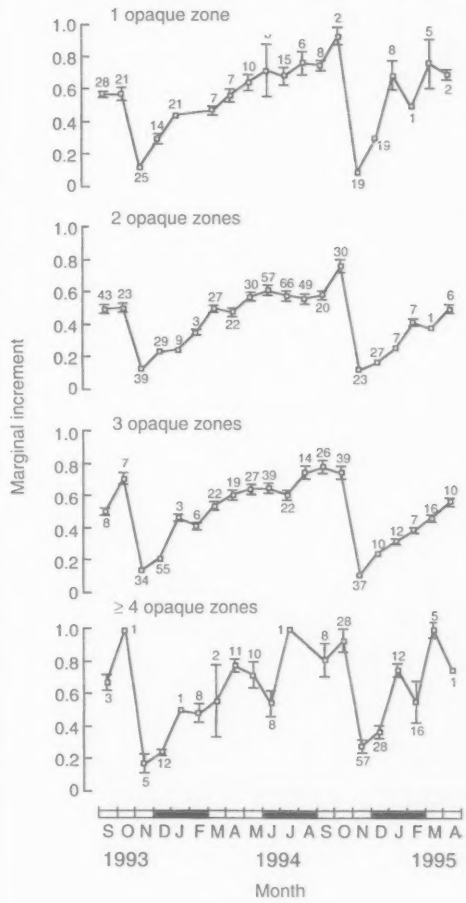

Figure 2

Mean monthly marginal increments ±1SE for sectioned sagittal otoliths of *Acanthopagrus butcheri* in the upper Swan River Estuary. The mean marginal increment is expressed as a proportion of the distance between the primordium and the edge of the opaque zone, when only one such zone was present, and as a proportion of the distance between the outer edges of the two outermost opaque zones, when two or more such zones were present. Sample sizes are given for each month.

Number of growth zones on hard structures

The number of opaque zones detected on a sectioned otolith of *A. butcheri* was always the same as the number observed on the same otolith prior to sectioning, when six or less such zones were visible on the whole otolith (Fig. 3A). However, the use of whole otoliths would have underestimated by one year 15% of seven- and eight-year-old fish, collectively, and, by one or two years, 57% of nine- to 13-year-old fish, collectively. The use of whole otoliths would also have underestimated the age of two 14-year-old fish by three years, two 15-year-old fish by two years, and one 19- and one 21-year-old fish by five years each (Fig. 3A).

The numbers of annuli observed on the scales of *A. butcheri* differed from those recorded in 27, 67, and 40% of the sectioned sagittal otoliths of the same fish, when the otoliths possessed one, two, and three opaque zones, respectively (Fig. 3B). The number of annuli exceeded that of the number of opaque zones in 34% of all cases. The number of annuli on the scales of fish, in which the sectioned otoliths possessed eight to eleven opaque zones, exceeded by one or two the number of opaque zones on those otoliths in 70% of cases (Fig. 3B). On the basis of the number of opaque zones on their sectioned otoliths, one fish that was estimated as 19 and another as 21 years old, displayed seven more annuli on their scales than on their otoliths. Although the number of sectioned otoliths with more than six opaque zones, that were used for comparisons with scales, was only 18, it is still noteworthy that the number of opaque zones on more than half of those otoliths was less than the number of circuli on the scales obtained from the corresponding fish.

The number of opaque zones recorded independently by a second "reader" for sectioned otoliths of *A. butcheri* with 0–3 zones (50 fish), 4–6 zones (50 fish) and 7–10 zones (40 fish), were always the same as those recorded by the senior author for the same otoliths. Furthermore, the second reader recorded the same number of opaque zones on all but two of the 22 sectioned otoliths that the senior author had recorded as having 11 or more opaque zones. Moreover, after reviewing and discussing the two discrepancies, the second reader agreed that he had failed to detect one of the least conspicuous opaque zones near the periphery of the two otoliths for which there were discrepancies, and therefore his counts agreed with the counts made by the senior author. However, the number of annuli counted on the scales by the second reader, that had previously been recorded by the senior author as having 0–3 annuli (50 fish), 4–10 annuli (30 fish), and ≥11 annuli (7 fish), differed in 20%, 43%, and 86% of cases, respectively, which reflects the difficulty in detecting annuli on scales. The differences between counts ranged from one on scales with 0–3 annuli to more than five on scales with ≥11 annuli.

Trends exhibited by length-frequency data for different age classes

The data presented earlier demonstrated that the number of opaque zones on whole otoliths of *A. butcheri* could be used for aging this sparid when there were six or less opaque zones present (Fig. 3A). However, the data in Fig. 3A showed that otoliths had to be sectioned to consistently reveal all of their opaque zones when they displayed seven or more such zones prior to sectioning. Thus, to reduce the margin for producing invalid counts to a minimum, estimates of the age of individual *A. butcheri* were made by using whole otoliths, when five or less opaque zones were present, and by employing sectioned otoliths, when six or more such zones were present.

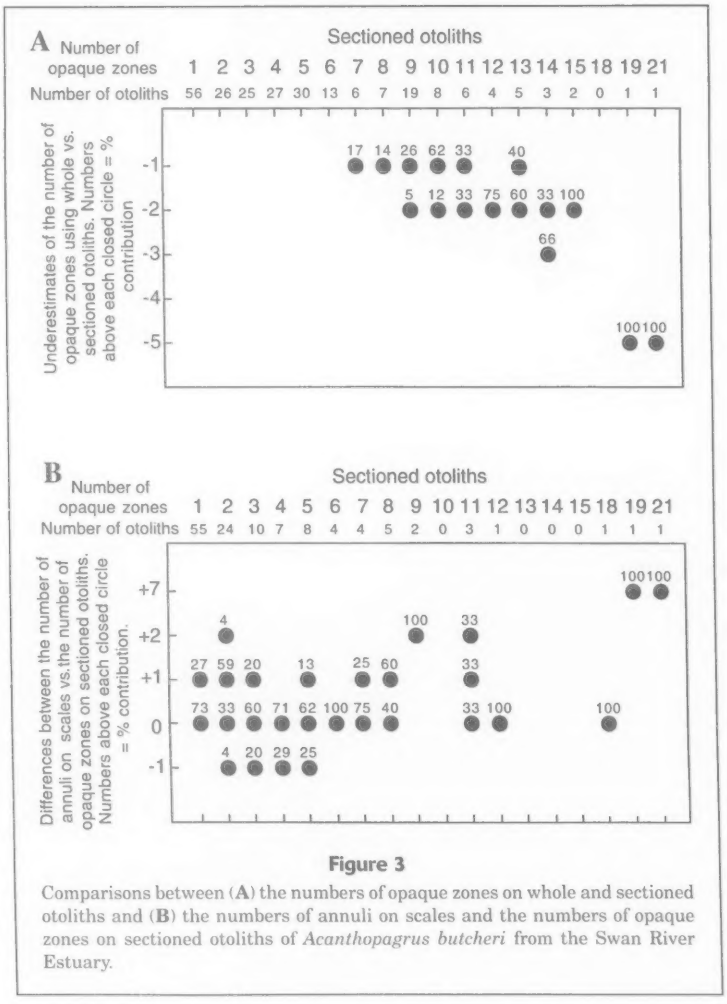
A
Sectioned otoliths
Number of opaque zones
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 18 19 21
Number of otoliths
56 26 25 27 30 13 6 7 19 8 6 4 5 3 2 0 1 1
Underestimates of the number of opaque zones using whole vs. sectioned otoliths. Numbers above each closed circle = % contribution
-1
-2
-3
-4
-5
17 14 26 62 33 40
5 12 33 75 60 33 100
66
100 100
B
Sectioned otoliths
Number of opaque zones
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 18 19 21
Number of otoliths
55 24 10 7 8 4 4 5 2 0 3 1 0 0 0 1 1 1
Differences between the number of annuli on scales vs. the number of opaque zones on sectioned otoliths. Numbers above each closed circle = % contribution.
+7
+2
+1
0
-1
100 100
4
100
33
27 59 20
13
25 60
33
73 33 60 71 62 100 75 40
33 100
100
4 20 29 25

Figure 3

Comparisons between (**A**) the numbers of opaque zones on whole and sectioned otoliths and (**B**) the numbers of annuli on scales and the numbers of opaque zones on sectioned otoliths of *Acanthopagrus butcheri* from the Swan River Estuary.

Although seine netting over sand in nearshore, shallow waters of the upper Swan River Estuary in the summer and early autumn of both 1993–94 and 1994–95 yielded many *A. butcheri* of 50 to 180 mm, it produced only a few smaller individuals of this species. However, sampling of beds of the macroalgae *Gracilaria verrucosa* in the same period in 1998–99 yielded considerable numbers of *A. butcheri* that ranged in length from 16 to 60 mm. Once *A. butcheri* reached lengths of ca. 60 mm, they moved from the beds of *G. verrucosa* to reside over sand. The lengths of these *A. butcheri*, which represented the 0+ recruits resulting from spawning from November to December of 1998 (Sarre and Potter, 1999), and thus represented the 1998 year class, increased from 16–32 mm in December 1998 to 26–63 mm in January 1999 to 44–86 mm in February 1999 and to 36–112 mm in March 1999 (Fig. 4). The mean length ±1SE in the latter month, i.e. 76 mm, did not differ significantly ($P>0.05$) from that of the 0+ age class in March 1994, when a substantial number of these small fish were also caught (Fig. 5).

Because *A. butcheri* spawns predominantly between October and January (spawning peaking in November [Sarre and Potter, 1999]), the cohort of small *A. butcheri* (81–115 mm), that was caught by seine net in the shallow waters of the Swan Estuary in September 1993 and whose otoliths did not possess an opaque zone, was the product of the spawning that took place in the spring to early summer of the previous year, i.e. 1992 (Fig. 5). The lengths of this 1992 year class increased from 81–115 mm in September 1993 to 100–152 mm in November 1993, by which time a single and narrow opaque zone could be discerned on the edge of the otoliths of this year class. Because spawning peaks in November, the members of this cohort were thus now about one year old. By November and December 1994, the lengths of this 1992 year class, now representing early 2+ fish, had increased to 170–220 and 189–224 mm, respectively. The 1993 year class first appeared in seine net catches in March 1994 at lengths of 67–102 mm and was caught until May, when its

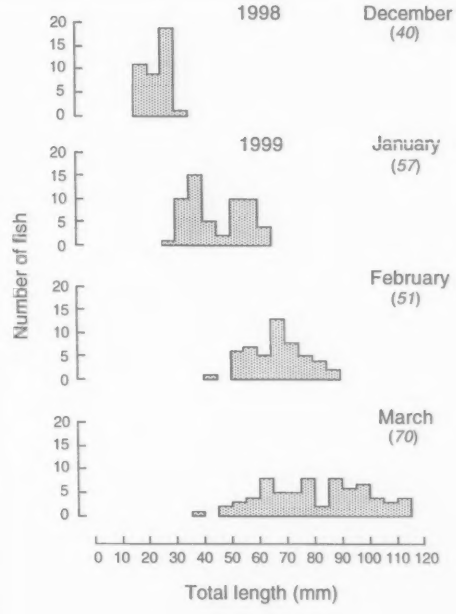

Figure 4

Length-frequency histograms for juvenile *Acanthopagrus butcheri* caught with a 5.5-m seine net (1-mm mesh) in the shallows (<1 m) of the upper Swan River Estuary between December 1998 and March 1999. Numbers in parentheses represent the number of fish measured.

lengths had reached 104–139 mm. When representatives of the 1993 year class reappeared in catches in September 1994, their lengths were still only 96–135 mm, indicating that growth had not occurred during the immediately preceding winter months. The lengths of the 1993 year class subsequently increased to between 136 and 183 mm in January 1995 (Fig. 5). Although the 1994 year class first appeared in March 1995, i.e. in the corresponding month to when the 1993 year class appeared in the previous year, its numbers were small and it was not represented in the following month, i.e. April (Fig. 5).

The 1991 year class was well represented in the majority of months (Fig. 5). The lengths of this strong cohort increased from 163–235 mm in September 1993 to 220–296 mm in September 1994 and to 222–325 mm in November 1994, at which time the fish were entering their fourth year of life. The 1990 year class was a particularly strong cohort (Fig. 5). The lengths of this year class increased from 208–304 mm in September 1993 to 268–349 mm in September 1994 and 259–360 mm at the commencement of their fifth year of life in November. The numbers of fish belonging to earlier year classes, i.e. the 1989, 1988, 1987 year classes, etc., were very low (Fig. 5). Thus, the number of older fish collectively in the Swan River Estuary was also low.

Maximum size and age and von Bertalanffy growth parameters

The spawning activity of *A. butcheri* peaked in early November in the Swan River, Moore River, and Nornalup Walpole estuaries and in early October in the Wellstead Estuary (Sarre and Potter, 1999). The von Bertalanffy growth curves for *A. butcheri* were thus derived by using a birth date of 1 November for the first three estuaries and 1 October for the Wellstead Estuary. Because many fully mature fish were found in Lake Clifton in early November, and this lake was located near the Swan River Estuary, a birth date of 1 November was likewise assigned to the population of *A. butcheri* in that system.

The lowest maximum lengths of female and male *A. butcheri* were 377 and 365 mm, respectively, which were recorded for fish caught in the Wellstead Estuary, whereas the greatest maximum lengths of each sex was 480 mm recorded for a female in the Swan River Estuary and 485 mm recorded for a male in Lake Clifton (Table 2). The maximum weights of *A. butcheri* in the five systems ranged from a low of 862 g for a female in the Wellstead Estuary to 2196 g for a female in the Swan River Estuary (Table 2). The maximum age of both sexes in each estuary was at least 15 years and the maximum age attained in any system was the 21 years recorded for both a female in the Swan River Estuary and a male in the Nornalup Walpole Estuary (Table 2).

The growth curves of male *A. butcheri* in the Swan River, Nornalup Walpole, and Wellstead estuaries and Lake Clifton followed similar overall trends and thus never crossed one another, and the same was true for the growth curves for females in the above three estuaries (Figs. 6 and 7). The rates of increase in the lengths of both sexes in the Moore River Estuary were initially slower than in each of the above three estuaries, and the rate of increase in the length of males in the Moore River Estuary was also initially less than that of this sex in Lake Clifton. (Note that there were insufficient data for the females in Lake Clifton to make similar comparisons with this sex in this system.) The far slower rate at which length initially increased in the Moore River Estuary is illustrated by the fact that, when male fish were 35–37 months old, i.e. three years in age, their mean length in this estuary was only 151 mm and significantly lower ($P<0.001$) than the 272 mm in the Swan River Estuary, 162 mm in the Nornalup Walpole Estuary, 204 mm in the Wellstead Estuary, and 339 mm in Lake Clifton. Likewise, the mean length of females of *A. butcheri* in the Moore River Estuary at this age was only 144 mm and thus significantly lower than the 285, 161, and 212 mm recorded in the Swan, Nornalup Walpole, and Wellstead estuaries, respectively. It is also noteworthy that the above-mean lengths of males in each of the five systems were significantly different from each other in all cases, except for *A. butcheri* from the Nornalup Walpole and Wellstead estuaries. Corresponding results were obtained for females in the four estuaries. As *A. butcheri* in the Moore River Estuary reached an older age, the growth curves for males and females in this estuary then crossed those for fish from the Nornalup Walpole and Well-

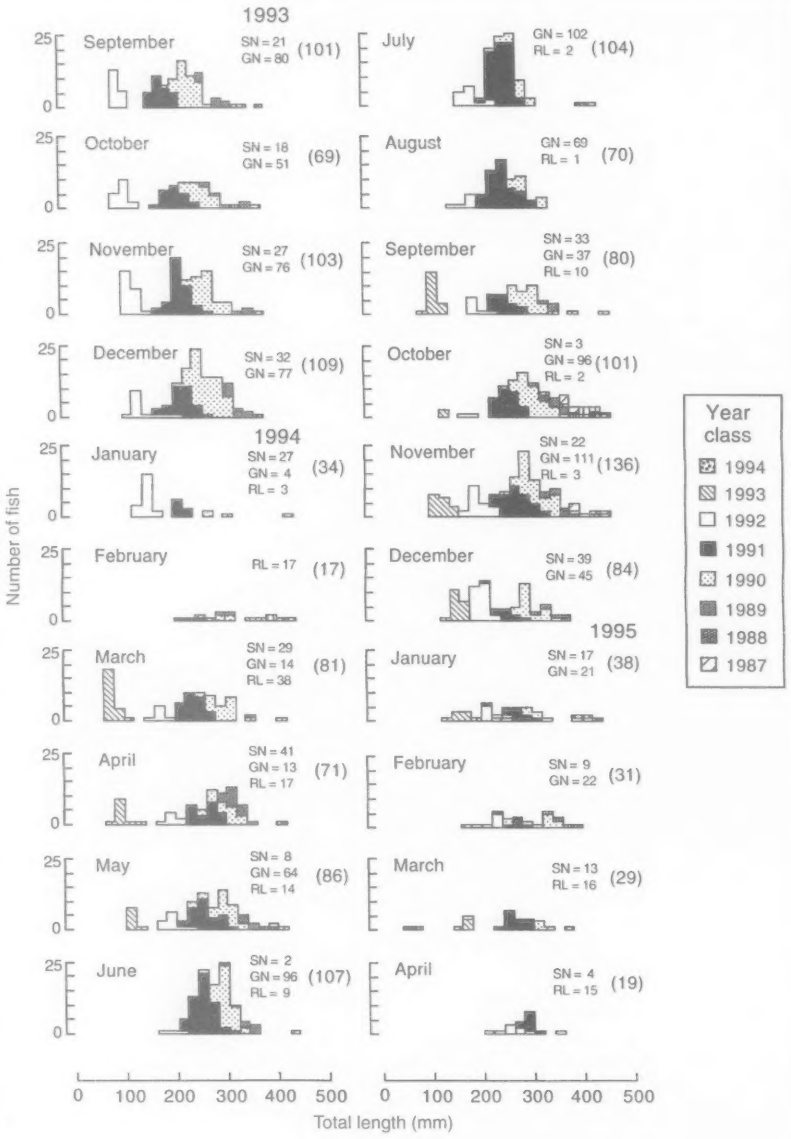

Figure 5

Length-frequency histograms for the different year classes of *Acanthopagrus butcheri*, with data derived from samples of males and females collectively that were caught with seine and gill nets in the upper Swan River Estuary between September 1993 and April 1995. Sample sizes in each month are given for seine netting (SN), gill netting (GN) and rod and line (RL) and in parenthesis for the total sample.

stead estuaries. This feature was reflected in significantly greater asymptotic lengths and lower k values for the Moore River Estuary population than those derived for fish in the latter two estuaries (Table 2, Figs. 6 and 7).

The likelihood ratio test demonstrated that neither the ages at length zero (t_0) nor the growth coefficients (k) in the von Bertalanffy growth equations differed significantly between female and male *A. butcheri* in either the

Table 2

Von Bertalanffy growth parameters and confidence intervals (95%) derived from length-at-age data for female and male *Acanthopagrus butcheri* caught in the Swan River, Moore River, Nornalup Walpole and Wellstead estuaries and for the males in Lake Clifton. n is sample size and L_{max}, W_{max}, and A_{max} are the maximum lengths (mm), weights (g), and ages, respectively. t_0 is the hypothetical age at which fish would have zero length, k is the growth coefficient, L_∞ is the asymptotic length and r^2 is the coefficient of determination.

					von Bertalanffy parameters			
	n	L_{max}	W_{max}	A_{max}	t_0	k	L_∞	r^2
Swan River								
Females	733	480	2196	21	−0.13	0.30	437.8	0.94
95% CL (lower)					−0.17	0.28	426.0	
95% CL (upper)					−0.10	0.31	449.5	
Males	894	475	1780	15	−0.15	0.31	419.3	0.94
95% CL (lower)					−0.19	0.29	10.7	
95% CL (upper)					−0.11	0.32	427.9	
Moore River								
Females	345	403	1192	17	−0.54	0.11	451.6	0.93
95% CL (lower)					−0.68	0.09	416.3	
95% CL (upper)					−0.41	0.12	486.9	
Males	387	394	1162	18	−0.61	0.11	429.2	0.92
95% CL (lower)					−0.76	0.09	395.9	
95% CL (upper)					−0.46	0.12	462.6	
Nornalup Walpole								
Females	346	412	1250	17	−0.60	0.16	367.0	0.91
95% CL (lower)					−0.88	0.14	352.5	
95% CL (upper)					−0.43	0.18	381.6	
Males	265	409	1148	21	−0.31	0.21	323.0	0.90
95% CL (lower)					−0.54	0.19	311.8	
95% CL (upper)					−0.08	0.24	334.6	
Wellstead								
Females	324	377	862	15	−0.17	0.25	377.8	0.91
95% CL (lower)					−0.27	0.23	365.3	
95% CL (upper)					−0.07	0.27	390.3	
Males	331	365	1247	15	−0.18	0.27	344.6	0.92
95% CL (lower)					−0.28	0.25	335.8	
95% CL (upper)					−0.08	0.29	353.4	
Lake Clifton								
Males	85	485	1914	18	−0.46	0.32	441.5	0.96
95% CL (lower)					−0.66	0.28	453.4	
95% CL (upper)					−0.26	0.36	429.6	

Swan River, Moore River or Wellstead estuaries (Table 3). Furthermore, although these two growth parameters did differ significantly between the two sexes in the Nornalup Walpole Estuary, the probability levels in both cases were close to 0.05. However, the asymptotic length (L_∞) for female fish was significantly greater than that of male fish in each estuary except that of the Moore River (Table 3).

The values for k and L_∞ for each sex differed significantly among the populations of *A. butcheri* in the four estuaries and between those of males in each of these estuaries and Lake Clifton ($P<0.001$ or 0.01). Furthermore, the values for t_0 for each sex almost invariably differed significantly ($P<0.001$ or <0.05) among the populations in the four estuaries and between those of males in each of these estuaries and Lake Clifton. Because the three von Bertalanffy parameters for both sexes were each shown almost invariably to differ significantly among the different populations, no attempt was made to test whether there was a common pattern of growth for each sex in each system.

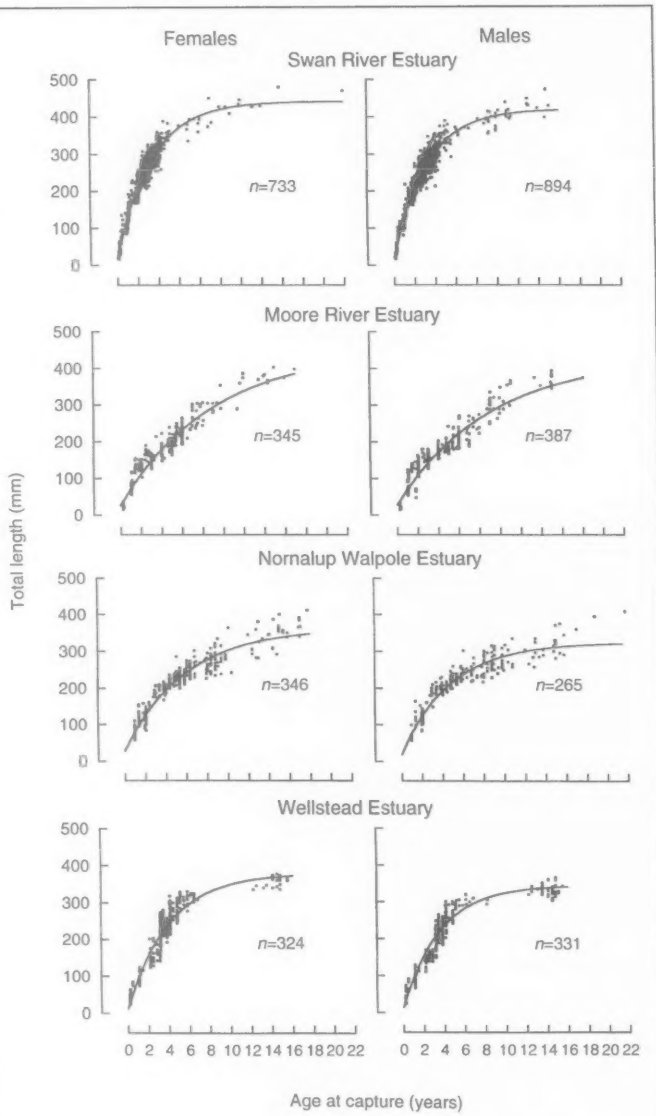

Figure 6

Von Bertalanffy growth curves fitted to length at age data for female and male *Acanthopagrus butcheri* caught in the Swan River, Moore River, Nornalup Walpole and Wellstead estuaries.

The values for k for *A. butcheri* were least in the Moore River Estuary, i.e. 0.11, and greatest in Lake Clifton, i.e. 0.32 (Table 2). The values for L_∞ ranged from a low of 367.0 mm for females and 323.0 mm for males in the Nornalup Walpole Estuary to a high of 451.6 and 441.5 mm for the corresponding sexes in the Moore River Estuary and Lake Clifton, respectively (Table 2). Estimates of t_0 for both sexes of *A. butcheri* in the four estuaries and of the males of *A. butcheri* in Lake Clifton all lay within the relatively narrow range of –0.13 to –0.61 years (Table 2).

Length–weight relationships

The equations relating total length and weight of female and male *A. butcheri* in each estuary and for males in Lake Clifton are presented below, so that, when required, the approxi-

mate weights of fish of a particular length can be estimated. Becasue analysis of covariance (ANCOVA) showed that neither the slopes nor the y-intercepts in the equations for female and male fish in each estuary differed significantly ($P>0.05$), the equations relating total length and weight for both sexes combined in each estuary are also presented.

Swan River Estuary		
Females:	$\log_{10} W = -5.09 + 3.14 \log_{10} L$	(r^2=0.99, n=865).
Males:	$\log_{10} W = -5.10 + 3.14 \log_{10} L$	(r^2=0.99, n=925).
Pooled:	$\log_{10} W = -5.07 + 3.14 \log_{10} L$	(r^2=0.99, n=1790).
Moore River Estuary		
Females:	$\log_{10} W = -5.10 + 3.13 \log_{10} L$	(r^2=0.99, n=250).
Males:	$\log_{10} W = -5.14 + 3.15 \log_{10} L$	(r^2=0.99, n=287).
Pooled:	$\log_{10} W = -5.12 + 3.13 \log_{10} L$	(r^2=0.99, n=537).
Nornalup Walpole Estuary		
Females:	$\log_{10} W = -4.99 + 3.07 \log_{10} L$	(r^2=0.99, n=302).
Males:	$\log_{10} W = -5.03 + 3.09 \log_{10} L$	(r^2=0.99, n=234).
Pooled:	$\log_{10} W = -5.00 + 3.08 \log_{10} L$	(r^2=0.99, n=536).
Wellstead Estuary		
Females:	$\log_{10} W = -4.84 + 3.01 \log_{10} L$	(r^2=0.99, n=274).
Males:	$\log_{10} W = -4.89 + 3.03 \log_{10} L$	(r^2=0.99, n=278).
Pooled:	$\log_{10} W = -4.85 + 3.02 \log_{10} L$	(r^2=0.99, n=552).
Lake Clifton		
Males:	$\log_{10} W = -5.12 + 3.14 \log_{10} L$	(r^2 =0.98, n=85).
Pooled:	$\log_{10} W = -5.10 + 3.13 \log_{10} L$	(r^2=0.99, n=100).

Discussion

Validation of the method for aging *Acanthopagrus butcheri*

Our study shows that a growth zone is not laid down in the otoliths of the 0+ age class of *Acanthopagrus butcheri* until winter and that this growth zone does not become clearly delineated until late spring. Because spawning peaks in early November in the Swan Estuary (Sarre and Potter, 1999), the first growth zone becomes delineated as the individuals of this species become one year old. Furthermore, the trends exhibited by the marginal increments on the sectioned otoliths of *A. butcheri* demonstrate that an opaque zone is laid down annually in this hard structure. Our results also demonstrate that the otoliths of *A. butcheri* do not need to be sectioned in order to consistently reveal all of the opaque zones until they had reached a size at which they possessed seven or more such zones. Validation that the opaque zones, which are revealed on the otoliths of *A. butcheri* by sectioning, are formed annually, implies that the estimates of the ages of individual black bream recorded by Morison et al. (1998) using sectioned otoliths are valid for fish caught in the Gippsland Lakes in eastern Australia. However, because the number of annuli on scales frequently differed from the number of opaque zones on sectioned otoliths from the same fish, the number of annuli on scales do not provide a reliable method for aging *A. butcheri*. Thus, those estimates of the age of individual *A. butcheri*, that have been based on the number of annuli on scales (Butcher, 1945; Thomson, 1957; Weng, 1971; Hobday and Moran[3]) are, in many cases, probably invalid.

Table 3

Significance levels for comparisons between the von Bertalanffy growth parameters for female and male *Acanthopagrus butcheri* caught in each of the Swan River, Moore River, Nornalup Walpole, and Wellstead estuaries by using the likelihood ratio test. ***=$P<0.001$, **=$P<0.01$, *=$P<0.05$, NS = Not significant. t_0 is the hypothetical age at which fish would have zero length, k is the growth coefficient, and L_∞ is the asymptotic length.

	von Bertalanffy growth parameter		
Estuary	t_0	k	L_∞
Swan	NS	NS	**
Moore	NS	NS	NS
Nornalup Walpole	*	*	***
Wellstead	NS	NS	***

Differences in age structures amongst populations

Because the majority of *A. butcheri* obtained from the Swan River, Moore River, Nornalup Walpole, and Wellstead estuaries were collected by using the same seine and

gill net sampling regimes, supplemented with a limited amount of angling, any gross differences in the age structure of samples from populations in the different estuaries almost certainly represent real differences. The percentage of *A. butcheri* caught at ≥5 years of age in the Swan River Estuary (5%) was far lower than in either the Moore River Estuary (30%), approximately 100 km farther north on the lower west coast of Australia, or the Nornalup Walpole Estuary (45%) on the south coast of Australia. Note that the estimate for the Swan River Estuary was restricted to data collected during the main sampling period and did not thus include the large samples of small fish that were caught between December 1998 and March 1999. The above differences in the proportion of older fish presumably reflect a greater "mortality" of older fish in the Swan River Estuary than in the other estuaries. It thus appears highly relevant that the population of *A. butcheri* in the Swan River Estuary is exposed to heavy fishing pressure from the recreational sector throughout the year and from commercial fishermen during winter and early spring, whereas the population in the Moore River Estuary is lightly fished and that in the Nornalup Walpole Estuary is not exposed to commercial fishing (Sarre and Potter, 1999).

Although representatives of all age classes up to 15+ were recorded for the populations of *A. butcheri* in each of the above three estuaries, this was not the case with the Wellstead Estuary, which is located 300 km to the east of the Nornalup Walpole Estuary. Thus, in the samples collected from this estuary in 1995 and 1996, the 1989, 1987, 1986, 1985, and 1984 year classes were not represented, and the 1988 year class was represented by only two fish (Fig. 6). This strong implication that, in the Wellstead Estuary, *A. butcheri* either does not spawn or has very limited spawning success in some years parallels the situation recorded for this species in the Gippsland Lakes in eastern Australia (Morison et al., 1998; Hobday and Moran[3]; Coutin et al.[4]). The work of Morison et al. (1998) demonstrated that, in that latter estuary, the commercial catches of *A. butcheri* between 1993 and 1996 were dominated by two year classes and that there had been no strong recruitment of *A. butcheri* since 1989. The absence or weakness of certain year classes in the Gippsland Lakes, and also in the Hopkins River Estuary which is also in eastern Australia, has been attributed to the detrimental influence on spawning success of such unfavourable environmental conditions as heavy freshwater discharge or unsuitable salinities (Newton, 1996; Hobday and Moran[3]). Thus, in the context of the absence of the 1984 year class in samples, it appears relevant that, in the Wellstead Estuary, which has normally remained closed during the last 30 years, there was, as a result of "cyclonic rainfall," an extremely protracted period of heavy freshwater discharge between the early spring of 1984 and the autumn of 1985 (Hodgkin and Clark[5]). This led to a very severe scouring of the substrate and a breaching of the bar at the mouth of this estuary, with the result that this mouth remained open between September 1984 and May 1985. The heavy freshwater discharge that occurred during and immediately after the 1985 spawning season of *A. butcheri* in the Wellstead Estuary would thus almost cer-

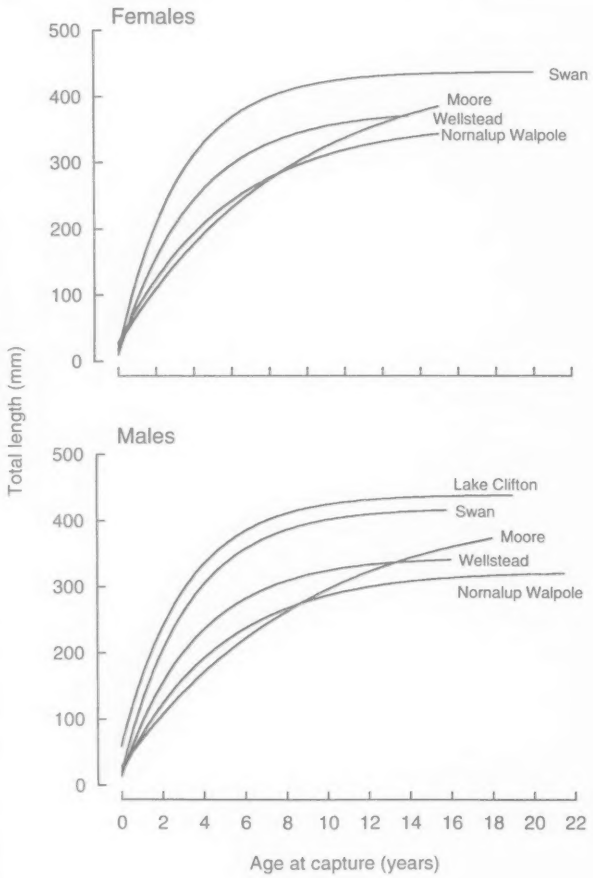

Figure 7

Comparisons between von Bertalanffy growth curves fitted to length-at-age data for female and male *Acanthopagrus butcheri* in the Swan River, Moore River, Nornalup Walpole, and Wellstead estuaries and for males in Lake Clifton in southwestern Australia.

[4] Coutin, P., S. Walker, and A. Morison. 1997. Black bream—1996. Compiled by the Bay & Inlet Fisheries and Stock Assessment Group. Fisheries Victoria Assessment Report 14. Melbourne, Victoria, Australia, 89 p.

[5] Hodgkin, E. P., and R. Clark. 1987. Wellstead Estuary, the estuary of the Bremer River. Estuarine Study Series 1. Environmental Protection Authority, Perth, Western Australia, 22 p.

tainly have flushed out to sea any eggs or larvae of this species that were produced during that period. However, it should also be recognized that freshwater discharge was so strong during that period that even many large *A. butcheri* were flushed out of the estuary, with the result that some of these fish were subsequently caught by anglers along the nearby coast (Spurr[6]). Furthermore, when freshwater discharge is very high, the salinities fall to such low levels that they are unlikely to be conducive to spawning by *A. butcheri* (Haddy and Pankhurst, 2000). Thus, the absence of the 1984 year class in samples may be due to the loss of eggs, larvae, or maturing and mature fish to the ocean in 1984, or to the inhibitory effect of low salinities on spawning, or to a combination of the latter.

The fact that the 1985 year class of *A. butcheri* was also not caught may reflect a low return of large *A. butcheri* to the estuary by the commencement of the spawning period in 1985. The absence of the 1986, 1987, and 1989 year classes and the paucity of the 1988 year class can probably be attributed to the fact that, although freshwater discharge was not as strong as in 1984, it was still sufficient to breach the bar at the estuary mouth during the spawning period in each of those years (Spurr[6]). It would thus also have been likely to result in a loss to the ocean of eggs and larvae produced during the spawning periods in those years or to the emigration of maturing or mature fish, or in both of these effects (Hodgkin and Clark[5]). The view that heavy freshwater flushing or very low salinities, or both, were the main contributors to the lack of spawning success of *A. butcheri* between 1984 and 1989 is consistent with the observation that, when freshwater discharge was not sufficiently strong to breach the estuary mouth, as was the case between 1990 and 1995 (Spurr[6]), there was at least a reasonable recruitment of each of the 1990 to 1995 year classes.

Comparisons between von Bertalanffy growth parameters for females and males

The likelihood ratio test showed that the growth coefficients (k) for female and male fish were significantly different in only one of the four estuaries, i.e. the Nornalup Walpole Estuary, and even then the probability level was close to 0.05, which is consistent with the fact that the values for the 95% confidence intervals for this parameter for the two sexes overlap in each estuary other than the Nornalup Walpole Estuary. The lack of a marked distinction between the growth rates of female and male fish is hardly surprising because *A. butcheri* undergoes a substantial amount of growth before the gonads start to become mature for the first time (Sarre and Potter, 1999). However, the maximum length and asymptotic length (L_∞) were always greater for female than male fish in each of the four estuaries, thereby paralleling the situation with many other fish species in both southwestern Australia (Laurenson et al., 1994; Wise et al., 1994; Hyndes et al., 1996; 1998) and elsewhere (e.g. Kenchington and Augustine, 1987; McPherson, 1992; Crabtree et al., 1995).

[6] Spurr, P. 1995. Local resident and former commercial fisherman. Personal commun. Bremer Bay, Western Australia.

The relatively low values determined for age at length zero for the two sexes in the four estuaries and for males in Lake Clifton, i.e. –0.13 to –0.61 years, reflects in part the good fit of the growth curves to the points for the age at length of the small fish. These low values for t_0 contrast with the –5.21 years for females and –3.70 years for males that were calculated by Morison et al. (1998) for *A. butcheri* in the Gippsland Lakes. Furthermore, the fork lengths at age zero for female and male fish in the Gippsland Lakes were ca. 110 and 100 mm, respectively. Thus, the von Bertalanffy growth equations recorded for *A. butcheri* in the Gippsland Lakes do not provide a good description of the pattern of growth throughout the full size range of fish.

Variations in von Bertalanffy growth parameters among populations

Although the patterns of growth of female and male *A. butcheri* in the Swan River, Wellstead, and Nornalup Walpole estuaries followed the same overall trends, with length increasing rapidly with time initially and then forming asymptotes, the values for k and L_∞ for each sex varied significantly amongst the populations in those estuaries. The initial rate of increase in length in these three estuaries was greatest in the Swan River Estuary and least in the Nornalup Walpole Estuary. Although the value for k for male *A. butcheri* in Lake Clifton differed significantly from that of this sex in the Swan River Estuary, the same was not true for L_∞. However, the value for L_∞ for male *A. butcheri* in Lake Clifton was still similar to that of this sex in the Swan River Estuary. The above comparisons demonstrate that the growth rate in Lake Clifton was similar to that in the Swan River Estuary, which is located only ca. 90 km farther to the north (see also Fig. 1). The von Bertalanffy growth parameters demonstrated that male *A. butcheri* grew more rapidly and attained greater asymptotic lengths in the Swan River Estuary and Lake Clifton than in either the Wellstead or Nornalup Walpole estuaries. The presence of faster growth rates in the Swan River Estuary and Lake Clifton, which are located at latitudes of ca. 32° on the lower west coast of Australia, than in the Nornalup Walpole and Wellstead estuaries, which are situated much farther south at a latitude of ca. 34° on the south coast of Western Australia, may reflect the greater temperatures found in more northern regions.

The pattern of growth of *A. butcheri* in the Moore River Estuary differed from those of this species in each of the other three estuaries and Lake Clifton, in that the increase in length with time was initially slower and the growth curve did not exhibit a marked asymptote. This pattern suggests that some factor or factors were less than optimal for growth during the first few years of life, but that conditions for growth improved later in life. The slow initial rates of increase in length of *A. butcheri* in the Moore River Estuary during early life may be related to the exceptionally high densities of this species in nearshore, shallow waters, the region which constitutes the typical habitat of the juveniles of this species (Sarre, 1999). The far greater density of this species in these waters, than in correspond-

ing waters of the other three estuaries, can be gauged from the fact that, during summer, the densities in such waters sometimes reached 234 fish per 250 m^2 in the Moore River Estuary, whereas they never exceeded 50 fish per 250 m^2 in any of the other three estuaries. Because *A. butcheri* tends to move into offshore and deeper waters as it increases in size, as is the case with several other fish species in southwestern Australian estuaries (Chubb et al., 1981; Chrystal et al., 1985; Potter et al., 1988; Wise et al., 1994), it then becomes more widely dispersed.

Although the high densities of juvenile *A. butcheri* in nearshore, shallow waters of the Moore River Estuary could have contributed to the initially slow rate at which length increased early in life, it also seems possible that the low salinities, i.e. generally <7‰ (Young et al., 1997), and quality of food in this estuary may also have had an inhibiting influence on the rate at which length increased. The view that low salinity has had such an effect is based on a combination of the results of detailed laboratory trials, which demonstrated that *A. butcheri* did not grow as well at 0‰ and 12‰ as at 24‰ (Sarre et al.[7]) and the fact that the upstream regions of other estuaries, where juvenile *A. butcheri* are located between late spring and early autumn when most growth occurs, are characterized by elevated salinities (Potter and Hyndes, 1994; Sarre, 1999). Although low salinities may restrict growth, it is worth noting that growth in the Wellstead Estuary, which was the only estuary to become hypersaline, was greater than in the Nornalup Walpole Estuary, which is likewise located on the south coast of Western Australia. However, as mentioned earlier, growth in the Wellstead Estuary was not as great as in the Swan River Estuary and Lake Clifton farther to the north.

In the context of potential food, it may be relevant that juvenile *A. butcheri* feed to a greater extent on algae in the Moore River Estuary than in other estuaries. As pointed out by Blaber (1974) during his study of another sparid, *Rhabdosargus holubi*, which likewise ingests a large amount of algal material, the volume of digestible material consumed is small. However, as *A. butcheri* increased in size in the Moore River Estuary, it fed to an increasing extent on whole large bivalves (Sarre et al., 2000), a food source that has a particularly high energy content (Whitfield, 1980).

The age compositions recorded in this paper for *A. butcheri* in different water bodies have been combined with data on reproductive biology to determine the lengths and ages at which black bream typically reach maturity in these systems, i.e. the L_{50} and A_{50} (Sarre and Potter, 1999). The resultant data showed that, amongst the estuarine populations, the A_{50} for female *A. butcheri* was lowest in the Swan River Estuary (2.2 years), in which the growth was greatest, and greatest in the Nornalup Walpole Estuary (4.3 years), in which early growth was relatively slow and the asymptotic length the least. The minimum legal length (MLL) for the capture of *A. butcheri* in southwestern Australia, i.e. 250 mm, is attained as early as 2.7 years in the Swan River Estuary and as late as 6.5 and 6.8 years in the Nornalup Walpole and Moore River estuaries. Because the MLL is well above the L_{50} for females and males of *A. butcheri* at first maturity in each system, it allows a substantial number of the members of each population to reach maturity before they are likely to be caught by either recreational or professional fishermen. However, the relatively small contribution made by *A. butcheri* ≥5 years old in the heavily fished Swan River Estuary emphasizes the need to keep the upper part of that estuary closed to commercial fishing and suggests that similar measures may be necessary in other estuaries as they become more heavily fished in the future.

[7] Sarre, G. A., G. J. Partridge, R. C. J. Lenanton, G. I. Jenkins, and I. C. Potter. 1999. Elucidation of the characteristics of inland fresh and saline water bodies that influence growth and survival of black bream. Fisheries Research and Development Corporation. Research Report, Project 97/309. Canberra, ACT, Australia, 68 p.

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Dispersal and growth of yearling Atlantic sturgeon, *Acipenser oxyrinchus*, released into Chesapeake Bay*

David H. Secor
Edwin J. Niklitschek
Jill T. Stevenson
Troy E. Gunderson

Chesapeake Biological Laboratory
University of Maryland Center of Environmental Science
1 Williams Street
Solomons, Maryland 20688

Steven P. Minkkinen
Brian Richardson
Benjamin Florence

Fisheries Division
Maryland Department of Natural Resources
580 Taylor Avenue B-2
Annapolis, Maryland 21401

Michael Mangold
Jorgen Skjeveland

U.S. Fish and Wildlife Service, MFRO
177 Admiral Cochrane Drive
Annapolis, Maryland 21401

Anne Henderson-Arzapalo

U.S. Geological Survey
Leetown Science Center
1700 Leetown Road, Kearneysville, West Virginia 25430

Abstract–Significant fisheries for Chesapeake Bay Atlantic sturgeon, *Acipenser oxyrinchus*, have been absent for nearly a century, and there has been no evidence of recovery in the intervening years. Endangerment of Atlantic sturgeon in the Chesapeake Bay has stimulated interest in aquaculture-based restoration programs. A critical and unknown issue is whether hatchery released fish would encounter habitats that support growth and survival. In July 1996, approximately three thousand Atlantic sturgeon yearlings were released into Nanticoke River (Maryland) and subsequently tracked to evaluate their growth and dispersal. Biotelemetry of 32 individuals showed down-estuary emigration into the Chesapeake mainstem habitat during summer and fall at average ground speeds below 0.5 km/d. During the first year after release, 262 yearlings were captured by commercial fishermen. All yearlings and two-year-old fish were determined to be of hatchery origin (8% capture rate). Yearlings were captured throughout the Chesapeake Bay mainstem and tributaries. Two released sturgeon were captured in the Albemarle Sound System (Chowan River, NC). Juveniles captured during summer and fall experienced ca. 1.5% daily specific growth rate. Diets comprised annelid worms, isopods, amphipods, and mysids. Wide dispersal, high incidence of feeding, and positive growth rates suggested that hatchery-produced juveniles dispersed to areas that supported consumption, growth, and survival. Because the Chesapeake Bay continues to support juvenile habitats, we propose that curtailed or absent spawning stock or spawning habitat, or both, are principal factors that have contributed to lack of Atlantic sturgeon recovery during the twentieth century.

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In Chesapeake Bay, Atlantic sturgeon, *Acipenser oxyrinchus*, may be functionally extirpated (Secor[1]; Speir and O'Connell[2]). Although sporadic observations of yearlings and adults have been reported over the last two decades (Colligan et al., 1998), the probability of population extirpation based upon the infrequency of these observations, is high (Grogan and Boreman, 1998). Depletion of Atlantic sturgeon in the Chesapeake Bay followed a period of high exploitation in the late 19th century (Fig. 1), during which overfishing occurred for most Atlantic sturgeon populations (Murawski and Pacheco, 1977; Secor and Waldman, 1999). Also, sedimentation and eutrophication have dramatically affected the Chesapeake Bay's environment during the past century (Officer et al., 1984; Cooper and Brush, 1991), resulting in loss and degradation of spawning and nursery habitats that may have contributed to loss in viability of sturgeon populations.

* Contribution 3335 of the University of Maryland Center for Environmental Science, Chesapeake Biological Laboratory, 1 Williams StreetSolomons, Maryland 20688.

[1] Secor. D. H. 1995. Chesapeake Bay Atlantic sturgeon: current status and future recovery. Unpubl. manuscript. Chesapeake Biological Laboratory, P.O. Box 38, Solomons, MD 20688-0038, 10 p.

[2] Speir, H., and T. O'Connell. 1996. Status of Atlantic sturgeon in Maryland's Chesapeake Bay. Unpubl. Manuscript. MD Dep. Natural Rrsources, Tawes State Office Building, 580 Taylor Avenue, Annapolis, MD 21401, 7 p.

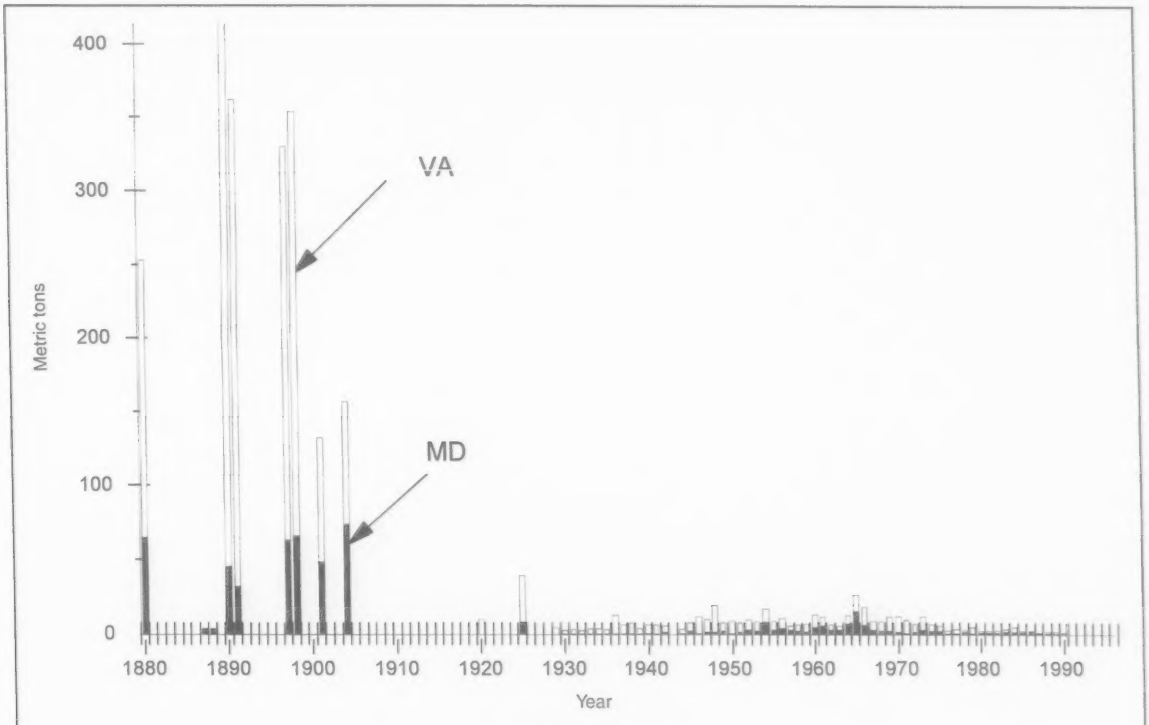

Figure 1

Atlantic sturgeon landings in Chesapeake Bay. Data from Murawski and Pacheco (1977) and Colligan et al. (1998). VA = Virginia; MD = Maryland.

During their first year of life, Atlantic sturgeon remain close to their natal habitats within estuaries (Dovel and Berggren, 1983; Bain, 1997). Following spawning migrations by adults, benthic eggs are deposited on hard, structured surfaces (e.g. cobble) in regions between the salt front and fall-line of large rivers. Historically, Chesapeake Bay Atlantic sturgeon spawned during April–June (Hildebrand and Schroeder, 1927). Young hatch at ca. 4–6 days after spawning, and following a 7–10 d period swimming upriver, adopt a benthic lifestyle (Smith et al., 1980). Young-of-the-year juveniles initiate seasonal migrations within estuaries (Dovel and Berggren, 1983). Emigration from natal estuaries to primarily marine habitats occurs at ages 1 to 5 years, after which subadults wander among coastal and estuarine habitats until maturation, undergoing rapid growth rates (Dovel and Berggren, 1983; Stevenson and Secor, 2000).

Lack of strong evidence of natural recovery has lead state, federal, academic, and nonprofit organizations to consider an aquaculture-based restoration program for Atlantic sturgeon in the Chesapeake Bay. To examine the feasibility of such a program, 3275 hatchery-produced yearlings (Hudson River progeny produced from a single female and four males) were released into the Nanticoke River (Chesapeake Bay) and their subsequent dispersal and growth was monitored over a one-year period. Specifically, we 1) characterized the dispersive behavior of non-native (hatchery-produced) Atlantic sturgeon yearlings through biotelemetry and the capture of sturgeons by fishermen, 2) explored potential relationships between the observed distribution and abiotic environmental factors, and 3) compared growth rate and diet of released juveniles observed in our study to those reported in the literature for naturally produced sturgeon.

Methods

Juvenile Atlantic sturgeon were obtained from the U.S. Fish and Wildlife Service (USFWS), Northeast Fishery Center, Lamar, Pennsylvania. During June 1995, Center personnel collected a large female (2.4 m total length) and three male Atlantic sturgeons from the Hudson River near Hyde Park (river km [rkm] 135). Fish were transported to the Center for artificial spawning and larval rearing. Larvae and early juveniles were reared in fresh water at 17°C and fed *Artemia* nauplii until 30 days after hatching. Juveniles (0.7–2.0 mm diameter) were then fed Biokyowa© fry feed *ad libitum* during their first year of life. A failure of the water heating system at the Center resulted in loss of temperature control, and juveniles >45 days after hatching, were subjected

Table 1

Capture data of coded wire tagged (CWT) and Floy-tagged Atlantic sturgeon, Chesapeake Bay 1996. 95% confidence intervals, based upon a binomial distribution, are given for the proportions of experimental groups in the capture sample. Note that because most fish were captured without T-tags and relatively few fish were sacrificed for CWT information, most of the 262 captures were not identified for release site or size class. Size at stocking could not be evaluated for differences in recapture rate due to small sample size.

Release site or size at stocking	Number released	% total released	Number identified from 262 captures	% group membership in capture sample (±95% CI)
Vienna (rkm 36)	1657	51	61	51 ±9
Sharptown (rkm 50)	1618	49	57	49 ±9
Total	3275		118	
Size class I (6–15 cm TL)	2306	70		
Size class II (22–36 cm TL)	969	30		
Total	3275			

to water temperatures of 10°C. At 6 months of age, ca. 1000 juveniles were transferred to Maryland and reared at 17°C at Maryland Department of Natural Resources (Maryland-DNR) and Potomac Electric Power Company hatchery facilities (Charles County, MD). Owing to differences in rearing temperature between juveniles held in Pennsylvania and Maryland hatcheries, two size classes resulted. At time of stocking, size class I ranged between 6 and 15 cm TL. Size class II ranged between 22 and 36 cm TL.

All stocked sturgeon were injected with an internal coded wire tag (CWT) to identify size class and stocking site. In tank-rearing studies conducted at the MD-DNR hatchery, CWT retention was >95%. Size class II juveniles were also tagged with external Floy T-tags inserted through their dorsal musculature below the fourth dorsal scute. Totals of 2306 and 969 juveniles from size classes I and II, respectively, were released into the Nanticoke River (MD) at river kilometers 36 and 50 on 7 July 1996 (Table 1, Fig. 2). River conditions at stocking sites were 0 and 3.0 ppt salinity, 26° and 27°C, and 4.2 and 7.7 mg/L dissolved oxygen (D.O.) at rkm 36 and 50, respectively. Site conditions varied less than anticipated in the study design, which stipulated release into divergent salinity levels because of high freshwater discharge rates to the Nanticoke River during spring and summer 1996.

Telemetry

To investigate short-term dispersal in the Nanticoke River, 32 juveniles were released at 5 sites over 7 occasions (Table 2) and tracked with Sonotronics© ultrasonic transmitters. Two size transmitters were used: 28 mm long by 8 mm diameter (2.5 g) and 64 mm long by 16 mm diameter (8 g) for Atlantic sturgeon <45 cm TL (released 7 July–12 August) and >45 cm TL (released 21 October), respectively. Both transmitters had a detection radius of 1 km; life spans were 60 days and 14 months for the small and large transmitters, respectively. Transmitters were attached by using a leather punch to drive 4.5-kg test monofilament through the third and fifth dorsal scutes. Line was affixed to the transistor by using a cyanocrylate glue, looped through the scutes and glued to the other end of the transmitter. A 50-day laboratory experiment on 10 dummy-tagged sturgeon showed 100% retention of transmitters with this method.

Table 2

Date and site of release of Atlantic sturgeon with ultrasonic transmitters, Nanticoke River, 1996.

Date	Release site	Number released	Number relocated	Mean length (cm) at release
8 Jul 96	rkm 36	3	2	39.2
	rkm 50	4	2	37.7
22 Jul 96	rkm 13	4	4	41.4
	rkm 36	4	4	40.9
12 Aug 96	rkm 24	3	2	39.2
	rkm 38	6	4	37.8
21 Oct 96	rkm 24	8	8	52.9
Sum		32	26	

Thirteen biotelemetry surveys were conducted throughout the Nanticoke River from July 1997 to February 1998. Tagged fish were located by using a hydrophone and identified by their coded signals. Position, temperature, salinity, and dissolved oxygen were recorded at each location site. On seven surveys, an otter trawl or 5-cm square gill net, or both, were deployed to capture juveniles that might be in the vicinity of the individual located through telemetry.

Relocation data were used to characterize overall displacement and to evaluate potential correlations with salinity, temperature, and dissolved oxygen conditions. Fish released at river kilometers 36 and 38 were com-

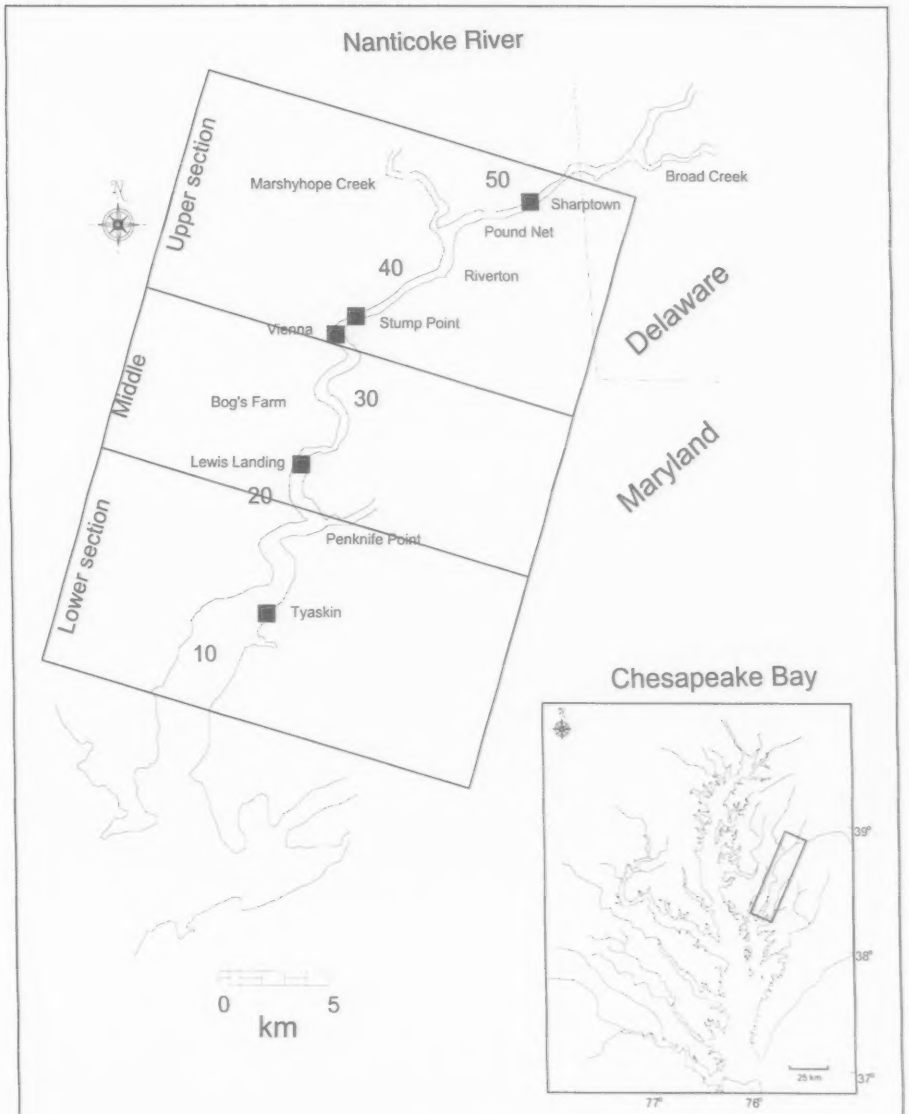

Figure 2

Map of Nanticoke River showing survey region, sites of release of yearling Atlantic sturgeon, and river sections utilized for statistical analysis. On 7 July 1996, >3000 yearlings were released at rkm 36 and 50. Later in summer and fall smaller releases of yearlings fitted with ultrasonic devices (Table 2) were made at rkm 13, 24, 36, and 50.

bined into a single group for statistical analysis. Consistency of mean trajectories and parallelism within and among released fish groups was tested by using multiple regression analysis, after modeling within-individual correlations (repeated measures) through a spatial power covariance model (Littel et al., 1996). Degrees of freedom were adjusted using Satterthwaite's approximation.

On the basis of upon multivariate analysis of available water quality data, the Nanticoke River was divided into three relatively homogeneous sections (Fig. 2): lower river: rkm 8 to 19.9, middle river: rkm 20 to 33.9, and upper river: rkm >34 (Table 3). Discriminate analysis indicated that this classification resulted in consistent differences in temperature, dissolved oxygen, and salinity records across

Table 3

Mean and standard deviations of measured environmental factors in Nanticoke River 8 July 1996–23 October 1996, by river section (see Fig. 2).

	River section			
Factor	Lower	Middle	Upper	Overall
River kilometers	8–19.9	20–33.9	34–59	8–59
Temperature (°C)	25.0 ±3.6	24.2 ±4.5	26.1 ±1.6	25.4 ±3.1
Dissolved oxygen (% saturation)	82.9 ±7.5	79.4 ±11.2	81.2 ±11.3	81.2 ±10.4
Salinity (ppt)	5.0 ±1.7	2.3 ±1.1	0.7 ±0.7	2.2 ±2.1
Depth (m)	2.9 ±1.1	5.8 ±2.1	5.8 ±2.5	5.1 ±2.4
Number of observations	32	35	60	125

summer and fall months (Wilk's approximated F, $P<0.001$). The upper river exhibited the highest mean temperature and salinities usually below 1 ppt. The middle section showed intermediate salinity (1–3 ppt), and highly variable temperature and dissolved oxygen conditions. The lower section corresponded to a shallow area with the highest salinity and dissolved oxygen means (Table 3, Fig. 3). Logistic regression analysis was used to explore potential relationships between probability of fish relocation within a river-section and corresponding water quality conditions.

Reward program

Maryland-DNR, in cooperation with USFWS and the Chesapeake Bay Foundation, offered a $25 reward to Chesapeake Bay fishermen for the capture and holding of live juvenile Atlantic sturgeon. The program was initiated in Maryland in July 1996 and extended to Virginia waters after February 1997. Capture data were documented by USFWS agents and measurements and tag information were recorded. In some instances, juveniles were sacrificed for CWT identification (n=22). Twelve of these fish, captured between 24 October 1996 and 8 January 1997, were made available to us for examination of diet (mean TL=56.1 cm ±7.40 SE; mean weight=823 g ±301.6 SE). Prey were classified at the lowest possible taxonomic level and evaluated according to numerical and volumetric contribution to diet.

Captured fish were measured for total length in mm (TL), fork length in mm (FL), and weight in g (W). Because all three measures were not consistently taken, we developed the following regressions to interconvert size measurements:

$$FL = 0.860 - 2.01\ TL \qquad (r^2=0.96, n=214) \quad (1)$$

$$\log_e W = -9.25 + 2.52 \log_e TL \qquad (r^2=0.64, n=211) \quad (2)$$

Growth was estimated by comparison of size at release (W_0) and size at capture (W_c) according to the formula

$$G_1 = (\ln W_c - \ln W_0)/t, \qquad (3)$$

where t = days after release.

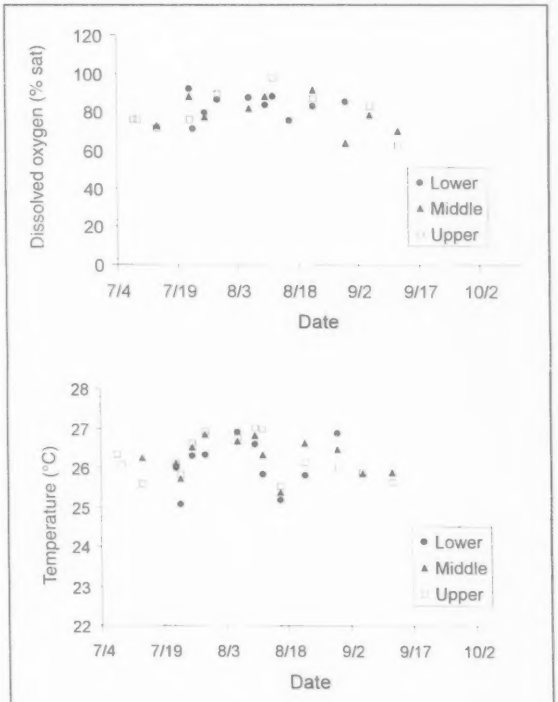

Figure 3

Mean records of (**A**) dissolved oxygen and (**B**) temperature by river section during summer 1996.

Results

Twenty-six fish were relocated during telemetric surveys at least once after release. The mean duration over which fish were tracked (35 days ±37 SD) and the number of relocations (4 relocations ±3.8 SD) were limited, perhaps owing to egress to the lower river and the Chesapeake mainstem (see "Discussion" section). Fish released at the

three most upstream sites (rkm 50, 36, and 24) showed a significant pattern of downriver displacement ($P<0.01$) at average ground speeds of 0.4 ±0.08 SE, 0.11 ±0.04 SE, and 0.08 ±0.02 SE km/day, respectively (Fig. 4). Fish released at rkm 13 did not show a consistent up or downriver movement ($P>0.9$). There were also significant differences in dispersal patterns between fish released at different dates within the same section. For instance, fish released 22 July at rkm 36, and 12 August at rkm 24 did not show a consistent downriver dispersal pattern.

The average probability of relocation tended to be higher in the middle section of the river (0.46 ±0.071 SE) than in the lower and upper sections, where average probabilities of relocation were 0.30 ±0.065 SE and 0.28 ±0.064 SE, respectively. However, such probabilities were not significantly different from each other, as indicated by logistic regression analysis ($P=0.13$). No significant correlations were found between dissolved oxygen, water temperature or salinity, and proportion of total relocations occurring within a given section ($P>0.11$). Although no significant correlation occurred between salinity and distribution of fish relocations, most fish had left freshwater areas (0 to 1 ppt) within one week of being released. More than 90% of later relocations occurred in the range 1 to 7 ppt. All attempts to capture sturgeon where position of fish was triangulated through biotelemetry were unsuccessful. In 25 bottom trawls and five gillnet deployments, only two cultured juveniles were physically captured, one in a gill net on 26 July (24 cm TL) and the other in an otter trawl on 24 October (43 cm TL).

During fall and winter (earliest capture 1 November 1996), fishermen captured juveniles as an incidental catch in the mainstem of the Chesapeake Bay. Location of captures varied seasonally (Fig. 5). During fall and winter months (November–March) most captures occurred in the vicinity of the mouth of the Nanticoke River and north of the Nanticoke River in the mainstem of Chesapeake Bay. As winter progressed, sturgeon captures were concentrated at upper Bay mainstem sites. The distribution of captures tended to spread toward the lower Chesapeake Bay and into tributaries during late winter (March) and spring months, where several sturgeon were captured high up in major tributaries (Patuxent, Potomac, Rappahannock, and James rivers). Much of the shift in captures during spring and summer may have been an artifact of delayed implementation of a reward program in Virginia (initiated February 1997) and seasonal changes in fishing effort (see "Discussion" section). In March 1997, two individuals were captured outside of Chesapeake Bay in the Chowan River (Albemarle-Roanoke estuary, North Carolina).

The majority of juvenile sturgeon (60%) captured by commercial fishermen were ensnared in drift or anchored gill nets set for striped bass, white perch (*Morone americana*), and catfish (*Ictalurus punctatus, Ameiurus catus*); 40% of the captures were from pound nets principally set for menhaden (*Brevoortia tyrannus*). Gillnet captures occurred most often between January and early March, with a mean capture length (TL) of 61 cm ±5.6 SE. Poundnet captures were concentrated between April and late June. Mean length for poundnet captures was 66 cm TL ±5.7 SE. Captured yearlings were kept for up to 2 days by fishermen, prior to inspection by USFWS agents, by holding sturgeon in pens and tanks, or by tying them (by the mouth or tail) to fixed structures in the water. Juveniles inspected by agents were all judged to be in good condition and released without apparent harm to the fish.

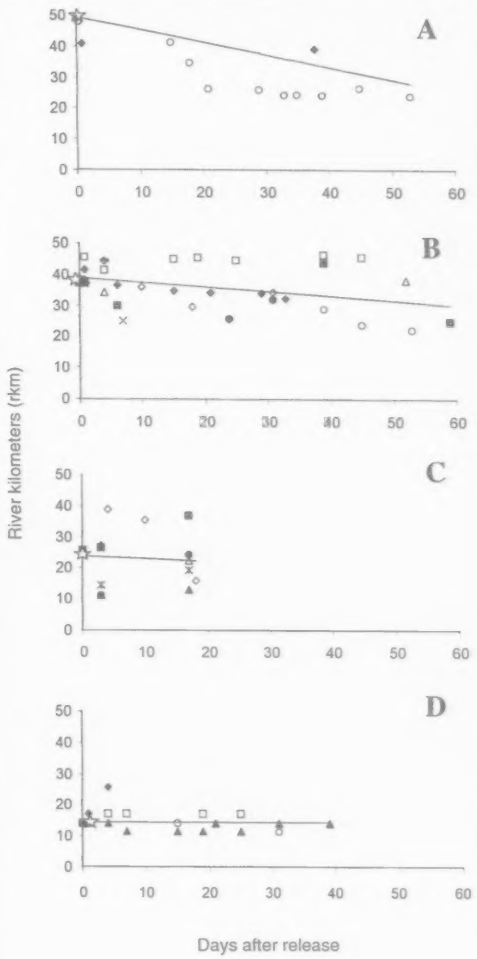

Figure 4

Relocation site (river kilometer) and mean trajectories for fish fitted with ultrasonic devices and released at different locations in the Nanticoke River. (**A**) release site 1 (rkm 50), (**B**) release site 2 (rkm 36–38), (**C**) release site 3 (rkm 24), and (**D**) release site 4 (rkm 13). Star icons indicate release site. Other icons within a graph indicate individual fish. Note that mean trajectories have been corrected for autocorrelation within individuals.

Overall, 8% of stocked juveniles were taken incidentally. Sixteen Floy-tagged juveniles (size class II) were multiple

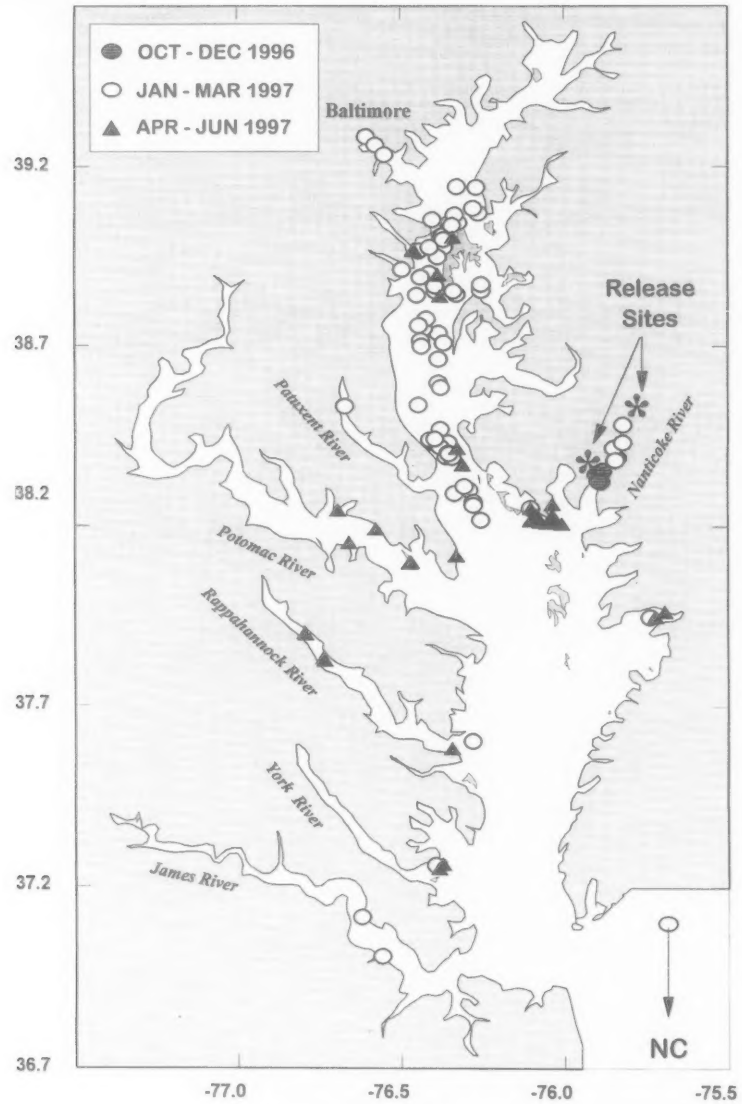

Figure 5

Spatial and temporal distribution of juvenile Atlantic sturgeon captures made by commercial fishermen in Chesapeake Bay.

recaptures but no fish were recaptured more than once. Capture rates of juveniles released at either up- or downriver sites were similar and indicated no differential survival between these groups (Table 1). All yearling sturgeon captured by fishermen contained a tag, or evidence of a lost tag. For those that had apparently lost a tag, a subsample of yearlings was determined to be of hatchery origin through analysis of microsatellite nuclear DNA.[3]

Released fish reached an average size of 67.2 cm TL ±3.8 (SE) and an average weight of 1536 g ±69 (SE), after 12 months in the wild (Table 4). Average growth rates, estimated from release to capture sizes, ranged between 0.64 and 1.83%/d. Estimated growth rates from monthly mean lengths and weights showed strong seasonality, with nil or negative growth rates between January and March (Fig. 6). One-third of the juveniles sacrificed for diet information had empty guts. Sand, silt, and detritus accounted for 34% of the combined gut contents. Of the remaining identified diet items, annelid worms were most important by volume

[3] King, T. 1997. Personal commun. Dep. of Interior, Leetown Science Center, 1700 Leetown Road, Kearneysville, WV 25430.

Table 4

Mean lengths and weights at ages 1 and 2 for juvenile Atlantic sturgeon observed in current study and reported in the literature.

Age 1 yr		Age 2 yr			
Fork length (cm)	Weight (g)	Fork length (cm)	Weight (g)	Geographical area	Source
20.0		25.0		St. Lawrence River	From Murawski and Pacheco (1977)
36.0		47.0		St. John River	From Murawski and Pacheco (1977)
40.8	500.0	47.7	770.0	Hudson River	Dovel and Berggren (1983)
28.4		43.9		Delaware River	Lazzari et al. (1986)
26.2	103.5	55.5	1535.8	Chesapeake Bay	Our study
57.8		74.4		Winyah Bay	Collins et al. (1996)
35.0		51.0		Suwannee River	From Murawski and Pacheco (1977)

(61%), followed by isopods (*Cyathura polita* and *Cyathura* sp., 23%), amphipods (*Leptocheirus plumulosus* and *Gammarus* sp., 10%), chironomid larvae (1.6%), and mysids (*Neomysis americana*, 1.5%). Occurrence data among yearlings indicated about 50% probability of finding all major food categories—worms, amphipods, and isopods—in feeding fish.

Discussion

Failure to capture a single wild yearling (<70 cm TL; see Peterson et al., 2000, for size criterion) during the course of our study is a strong indication of the Atlantic sturgeon's endangered status in Chesapeake Bay. In the fall of 1997, the floating carcass of a 2.6-m-TL female Atlantic sturgeon was observed in the James River.[4] Also, wild yearlings (<50 cm TL) were observed during 1998 in Virginia tributaries (Musick[5]) suggesting that some reproduction was still occurring in lower Chesapeake Bay. On the other hand, absence of yearling Atlantic sturgeon during Virginia Institute of Marine Science trawl monitoring over the past 15 years led Grogan and Boreman (1998) to predict >95% probability of extirpation in Virginia. Although this prediction has proven false, it still provides strong evidence of extremely depressed reproduction rates.

Results from our study indicated that the Chesapeake Bay can support nursery functions for juvenile Atlantic sturgeon. High capture rates by fishermen suggest high survival of released fish and high vulnerability to the gear types deployed. Wide dispersal and positive growth rates indicate that juveniles dispersed to areas that supported consumption and metabolic needs. Indeed, mean weight increased nearly 20-fold over the first year after release. Sizes at the end of the second year of life (summer 1997) were intermediate between size estimates for 2-year-old juvenile sturgeons from the Hudson River (Dovel and Berggren, 1983) and those from southern populations (Table 4). Thus, hatchery-produced fish had grown at levels that might be expected for juveniles naturally occurring in the Chesapeake Bay.

Although limited by a small sample size, our diet analysis seems consistent with the few published reports on food habits of juvenile Atlantic sturgeon. Aquatic insects, amphipods, isopods, and both polychaete and oligochaete worms are the most common items previously reported for juveniles residing in fresh and brackish waters (Vladykov and Greeley, 1963; Smith, 1985; Moser and Ross, 1995; Haley, 1998). Contrary to Vladykov and Greeley (1963) and Moser and Ross (1995), we found no evidence of juvenile sturgeon predation upon mollusks, which represent the highest biomass of benthic invertebrates in the Chesapeake Bay.

We failed to detect any significant selection among tracked individuals for certain water temperatures or dissolved oxygen conditions. Overall, tracked fish did not encounter severe hypoxia or extremely high temperatures (Table 3, Fig. 4). However, on at least one occasion, other than the day of release, yearlings encountered dissolved oxygen saturations close to 50% (4.3 mg/L, 25.9°C)—a level that might reduce growth and survival rates for this species (Secor and Gunderson, 1998). Preferential use of cooler areas or deep thermal refuges, or both, has been observed in field studies on juvenile Atlantic (Moser and Ross, 1995) and Gulf (Clugston et al., 1995) *A. oxyrinchus desotoi* sturgeons. Such refuges are unavailable in the Nanticoke River, a shallow system (Table 3) with little thermal stratification.

Low rates of use of habitats of salinity below 1 ppt agree with past observations that yearling Atlantic sturgeon principally use brackish water habitats (Dadswell, 1979; Brundage and Meadows, 1982; Smith, 1985; Moser and Ross, 1995; Haley et al., 1996). Observed down-estuary movement is consistent with seasonal movements reported for juvenile Atlantic sturgeon responding to summer peak temperatures in the Hudson River (Dovel and Berggren, 1983). Use of areas below rkm 10 was probably underestimated because river width substantially exceeded the detection range of ultrasonic transmitters and shallow reefs or sills probably obstructed detection.

[4] Spells, A. 1997. Personal commun. USFWS, 11110 Kimages Road, Charles City, VA, 23030.

[5] Musick, J. 1999. Personal commun. Virginia Institute of Marine Science, Gloucester, VA.

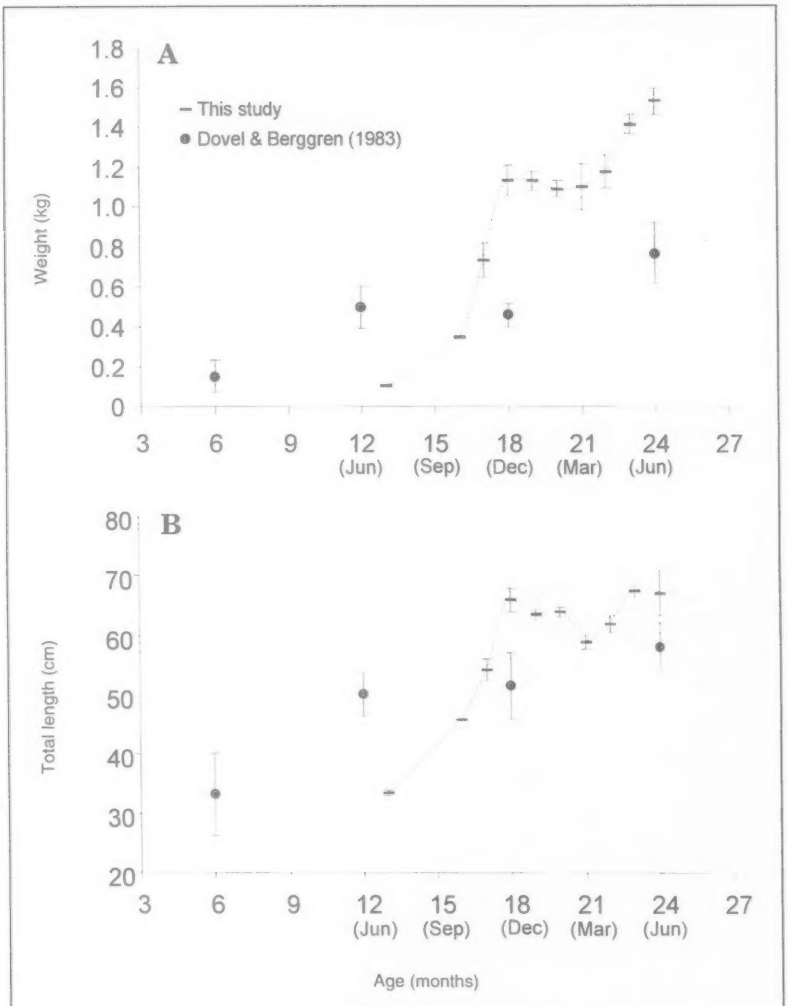

Figure 6

Growth curves as observed from released and captured juvenile Atlantic sturgeon in Chesapeake Bay. (**A**) Mean weight at age (month) ±SE. (**B**) Mean length at age (month) ±SE. Values reported by Dovel and Berggren (1983) are included for comparison. Note that Dovel and Berggren's data are averaged for all fish falling within a six-month age interval. Monthly values were fitted with a spline function (dashed line).

Tagging and telemetry studies on North American sturgeons (mostly on subadult and adult fish) tend to show seasonal or reproductive migrations but reduced displacements during intermigratory periods. Estimated home ranges for nonmigrating sturgeon were 0.8 km for landlocked white sturgeon (Haynes et al., 1978), 4 km for Gulf sturgeon (Clugston et al., 1995), and 2–3 km for shortnose sturgeon (Buckley and Kynard, 1985). Nonetheless, extensive wandering behavior was observed in adult shortnose sturgeon by McCleave et al. (1977), i.e. home ranges up to 30 km at average ground speeds around 0.21 body lengths (BL)/s. Moser and Ross (1995) observed gross movements ranging from 0.7 to 1.3 km/d in nonmigratory juvenile Atlantic sturgeon (68–122 cm TL) in Cape Fear River, NC. During seasonal or reproductive migrations, gross movement may increase to 0.8–7 km/d in juvenile (38–79 cm FL) Atlantic sturgeon (Gilbert, 1989), 0.6–6 km/d in Gulf sturgeon (Clugston et al., 1995), and 6.4–36 km/d in shortnose sturgeon (Buckley and Kynard, 1985; Kieffer and Kynard, 1993). We interpret our telemetry observations on initial yearling dispersal as a roving behavior, where fish are oriented toward searching for productive benthic

forage conditions. This is supported by the relatively low rates of dispersal (0–0.4 km/d; 0.1 BL/s), low horizontal gradient observed in abiotic parameters, and a lack of correlation between relocation probability and water quality data. More intensive sampling and benthic resource mapping in Chesapeake Bay could confirm this speculation.

A moderate reward system was highly effective in helping to evaluate the release of hatchery sturgeon. Although we expect more juveniles may have actually been captured than reported, fishermen were keenly interested in the program and very cooperative with USFWS agents in their collection of biological measures. High capture rates of yearling Atlantic sturgeon by fishermen showed that small sturgeons were highly vulnerable to gill and pound nets, as found by Collins et al. (1996). Due consideration needs to be given to incidental catches of juvenile-stage sturgeon in recovery programs.

Seasonal and spatial patterns of captures by fishermen were the result of both seasonal dispersal and distribution of fishing effort in Chesapeake Bay. In winter and early spring months, drift and anchor gill nets were set for striped bass, white perch, and catfish in the upper bay and in tributaries. Later in the spring and summer, pound nets were set for menhaden, croaker (*Micropogonias undulatus*), and spot (*Leiostomus xanthurus*), which tend to occur down-estuary. Therefore, the apparent displacement of captures from the upper to lower Chesapeake Bay may be related to seasonal changes in fishing effort. In addition, Virginia began a reward program in February 1997; therefore captures were less likely to occur prior to that date.

The dispersal of released fish into Chesapeake Bay mainstem by fall 1996 and reported captures in North Carolina by the end of the winter also are consistent with seasonal movement patterns described for Atlantic sturgeon in other systems. Seasonal migration in juvenile Atlantic sturgeon seems primarily regulated by changes in temperature gradients between fresh and brackish waters (Van Den Avyle, 1984). Juveniles tend to use brackish waters close to estuary mouths during the colder months as reported in Hudson River (Dovel and Berggren, 1983; Gilbert, 1989), Delaware River (Brundage and Meadows, 1982; Lazzari et al., 1986), and the Winyah Bay system (Smith et al., 1982). In the Hudson River, juveniles begin moving to saltier waters by July (Dovel and Berggren, 1983), whereas in the Delaware River many fish remain in tidal water until January (Lazzari et al., 1986). A different pattern was observed by Moser and Ross (1995), who noted that juvenile Atlantic sturgeon in the Cape Fear River kept the same center of distribution all year round.

High dispersal rates of released yearlings and absence of schooling behavior were somewhat unexpected. Hatchery-produced striped bass and Pacific salmon (*Oncorhynchus* spp.) juveniles are known to school and remain in restricted regions for weeks and months following release (Nickelson et al., 1986; Hume and Parkinson, 1987; Dorazio et al., 1991; Nagata et al., 1994; Andreasen, 1995). Recent genetic studies indicate strong population structuring within the geographic range of the Atlantic sturgeon (Waldman and Wirgin, 1998), which suggests high fidelity to natal estuaries. Gene flow studies also support consistent homing behavior by the Gulf subspecies (Wirgin et al., 1997). However, the rapid dispersal we observed might suggest that yearlings had insufficient opportunity to imprint to the Nanticoke River and thus might be unlikely to home to it in future spawning migrations. Apart from work on salmonids, little is known on homing behavior in anadromous fishes. In Pacific salmon, the window of imprinting occurs during the premigratory smolt stage (Hasler and Scholz, 1983). Stocking young-of-the-year Atlantic sturgeon in any future hatchery-based restoration program would be prudent because it might increase the duration of exposure to imprinting stimuli.

This study demonstrates that the Nanticoke River and Chesapeake Bay can continue to support nursery roles for Atlantic sturgeon yearlings. Still, several questions remain before we embark on a program of restoration through hatchery-based reintroduction. What are the main factors defining suitable habitat for Atlantic sturgeon juveniles? Would available habitat support historical abundances? Can we obtain sufficient numbers of brood stock from the Hudson River or elsewhere to ward against inbreeding depression? A critical question is whether released juveniles will return and find spawning habitat. Spawning habitats are probably quite degraded from siltation and sedimentation over the past two centuries. Unfortunately, evaluating whether such habitats remain or can be restored will be nearly impossible until an adult biomass can be restored.

Acknowledgments

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Growth rates of juvenile dusky sharks, *Carcharhinus obscurus* (Lesueur, 1818), from southwestern Australia estimated from tag-recapture data

Colin A. Simpfendorfer

Western Australian Marine Research Laboratories
PO Box 20
North Beach
Western Australia 6020, Australia
Present address: Center for Shark Research, Mote Marine Laboratory
1600 Ken Thompson Parkway
Sarasota, Florida, 34236
Email address: colins@mote.org

Abstract–Tagged neonate and small juvenile *Carcharhinus obscurus* were released between March 1994 and June 1996 in southwestern Australia. Length and time-at-liberty data from 304 usable recapture data were used to examine growth rates of male, female, oxytetracycline injected, noninjected, and all individuals combined. Recaptures were made up to 4.7 years after release. Four methods of analysis were employed: Gulland and Holt, Fabens, Francis, and length-at-age. Length-at-age analysis was possible because the majority of the animals released had open umbilical scars and so were of known age. The four methods produced varying results. One method was not able to estimate growth parameters, another produced inaccurate estimates of von Bertalanffy growth parameters, and two methods indicated that a linear growth model described growth better than the von Bertalanffy model. Although each produced different results, the three successful methods estimated that the growth rate up to age 5 ranged from 8 cm/year to 11 cm/year. These growth rates agreed closely with those reported for young *C. obscurus*. Length-at-age analysis indicated significant differences in the growth rates between males and females, and between oxytetracycline-injected and noninjected males. Results from the Francis method did not show significant differences between males and females, or injected and noninjected animals. The coefficient of variation of growth variability ranged from 0.24 to 0.40, mean measurement error ranged from 0.0 cm to 0.94 cm, and the standard deviation of measurement error ranged form 2.1 cm to 2.4 cm. The usefulness of each of the methods is discussed—the more detailed methods providing a better understanding of tag-recapture data.

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Tag-recapture data are a useful source of information on the growth of animals. The simplest form of analysis is to estimate an average growth rate, normally for a specific size range, from the period at liberty and the growth increment. This approach has been used in studies examining elasmobranch growth. For example, Thorson and Lacy (1982) estimated the average growth rate of adult sawfish (*Pristis perotteti*), Pratt and Casey (1983) provided average growth rates for shortfin mako sharks (*Isurus oxyrinchus*) in 20-cm size groups, and Casey et al. (1985) provided estimates of growth rates for sandbar sharks (*Carcharhinus plumbeus*) in 20-cm size groups. Although this approach provides information on growth rates that can be compared with those predicted by other techniques, it does not provide estimates of parameters for growth functions (e.g. the von Bertalanffy growth function).

A more useful approach is to fit growth functions to tag-recapture data. A range of techniques have been developed to undertake this type of analysis. Early techniques used relatively simple approaches (e.g. Walford, 1946; Gulland and Holt, 1959; Fabens, 1965) to estimate parameters of the von Bertalanffy growth function. Species of elasmobranchs for which these types of techniques have been used include three species of *Raja* (Holden, 1972), *C. plumbeus* (Wass, 1973; Casey and Natanson, 1992), *Galeorhinus galeus* (Grant et al., 1979), *Squatina californica* (Cailliet et al., 1992) and *Galeocerdo cuvier* (Natanson et al., 1999). With the advent and proliferation of powerful computers, more sophisticated techniques have been developed to deal with tag-recapture data and to allow the fitting of a range of growth functions and the estimation of confidence intervals (Francis, 1988). These growth functions have included both the widely used von Bertalanffy curve, as well as other forms (e.g. Schnute, 1981; Francis, 1995). In addition, functions that allow for the estimation of seasonal growth patterns (e.g. Francis, 1988), growth variability (e.g. Francis, 1988, Wang et al., 1995), and measurement error (e.g. Francis, 1988) have been developed. These more complex functions allow researchers to extract more information from tag-recapture data, as well as identify factors that may be important in determining the growth of individual animals. These types of analysis have not been widely used in elasmobranch studies to date. However, Francis and Francis (1992) and Francis and Mulligan (1998) used the Francis (1988) method for *Mustelus lenticulatus* and *G. galeus*, respectively.

Tagging studies of elasmobranch populations have also been used to validate age data based on vertebrae. Individuals are injected with a marker that is incorporated into calcifying structures so that the number of bands laid down between tagging and recapture can be determined, and the periodicity of band formation validated (Cailliet, 1990). The most commonly used marker in these studies is oxytetracycline (OTC) at dose rates of approximately 25 mg/kg (Gelsleichter et al., 1998). OTC is also a powerful antibiotic with recommended

daily doses of 10mg/kg for elasmobranchs (Stoskopf, 1993). Despite its antibiotic properties it has been demonstrated to have toxic effects on some teleosts (e.g. Marking et al., 1988). Although widely used, the impact of OTC injection on the growth of elasmobranchs has been poorly studied. Tanaka (1990) demonstrated that injection of OTC did not affect the growth of juvenile *Orectolobus japonicus* at normal dosages. Gelsleichter et al. (1998) reported that OTC injection did not affect the growth of nurse sharks (*Ginglymostoma cirratum*), but that it may have some level of hepatotoxicity. In the only reported study of a wild elasmobranchs, Natanson et al. (1999) reported that four *Galeocerdo cuvier* specimens injected with OTC did not have growth rates different from those not injected with OTC.

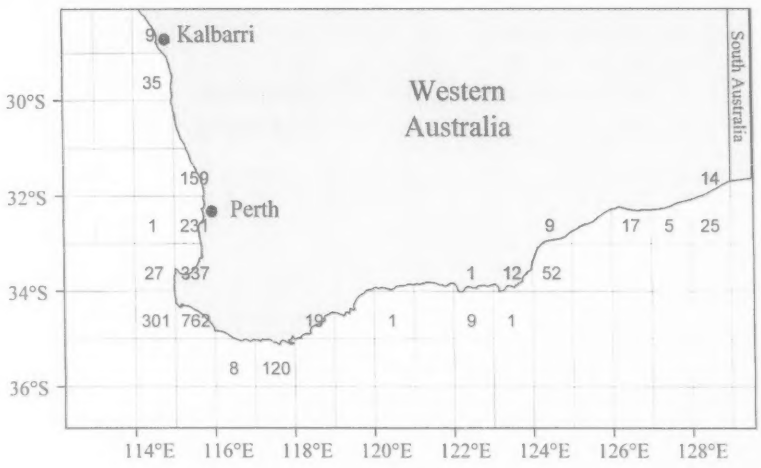

Figure 1

Numbers of juvenile *Carcharhinus obscurus* released in one-degree geographic blocks off southwestern Australia.

The dusky shark, *Carcharhinus obscurus*, is a large species of coastal shark that occurs in tropical, subtropical, and temperate oceans world-wide (Compagno, 1984). They are born at 70–100 cm total length (TL), mature at approximately 280 cm TL, and grow to at least 365 cm TL (Last and Stevens, 1994). Natanson et al. (1995) provided estimates of growth parameters for *C. obscurus* from the western North Atlantic, using length-at-age data and length-frequency data. These data indicate that *C. obscurus* is slow growing, reaches maturity at approximately 19–21 years, and possibly lives to 45 years. Natanson and Kohler (1996) estimated growth parameters for *C. obscurus* from the southwest Indian Ocean, using length-at-age data that indicated growth similar to that from the western North Atlantic.

A demersal gillnet fishery in southwestern Australia targets neonate and small juvenile *C. obscurus*, mostly from February to June. The fishery has operated since the 1940s, but significant catches of *C. obscurus* were not taken until the mid 1970s (Simpfendorfer and Donohue, 1998). Increasing fishing effort in the 1980s lead to concerns about the status of this resource and prompted a research project that included a tag and release study to estimate mortality (Simpfendorfer, 1999), movement, and growth parameters for *C. obscurus*. The aims of this paper are 1) to estimate growth rates and growth parameters for *C. obscurus* based on tag-recapture data using four different methods, 2) to investigate differences in growth due to sex or injection with OTC, and 3) to estimate growth variability and measurement error.

Materials and methods

Tagging

Neonate and juvenile *C. obscurus* were caught between March 1994 and June 1996 by commercial demersal gillnet vessels operating in southwestern Australia. These vessels operate in continental shelf waters in depths of 7–100 m. The gill nets are constructed of 16.5-cm and 17.8-cm (stretched) mesh monofilament netting that is 1.5 m to 2.0 m deep. Nets are 3–7 km in length and are set on the sea floor for periods of 7–24 hours.

Individual *C. obscurus* were measured (fork length [FL]: the distance from the tip of the snout to the caudal fork measured as a straight line) to the nearest centimeter, the sex of each fish was determined, and each fish was examined for the presence of an open umbilical scar, and tagged with an individually numbered Jumbo Rototag (Dalton Supplies, Woolgoolga, New South Wales, Australia) in the first dorsal fin. Approximately one in every three animals was injected with OTC (25 mg/kg) to mark the vertebral centra for age validation studies.

A total of 2199 juvenile *C. obscurus* were released from March 1994 to June 1996 between the Western Australian and South Australian border (129°E) and Kalbarri (29°S) (Fig. 1). Tagged sharks ranged in size from 53 cm FL to 108 cm FL but most were 70–81 cm FL (Fig. 2). One thousand seven hundred and thirty (78.7%) had open umbilical scars; 1062 were female, 1100 were male, and 37 were of unknown sex; 879 were injected with OTC and 1320 were not injected. Information on tag-recaptures, including date and location of recapture, and length were reported by commercial fishermen and research observers operating in the demersal gillnet fishery. Fishermen were provided with tape measures and trained to measure fork length in an attempt to improve the accuracy of recapture data.

Analysis

Growth rates of five groups of juvenile *C. obscurus*—males, females, OTC injected, non–OTC-injected, and all recaptures combined—were estimated by using four different

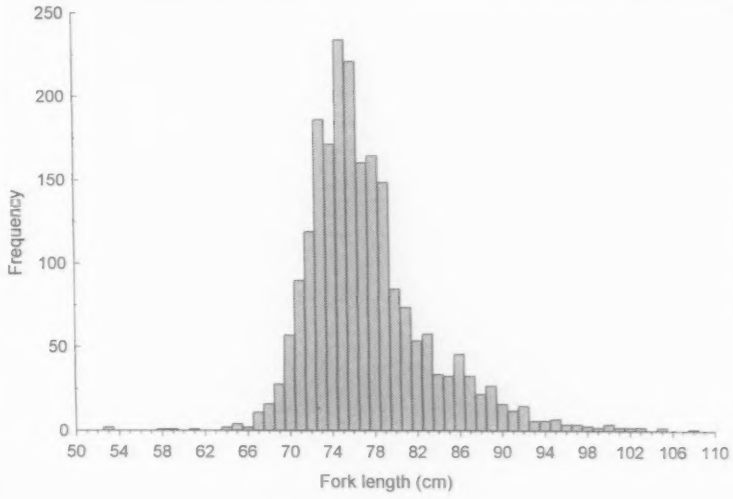

Figure 2

Size at release for 2199 juvenile *Carcharhinus obscurus* tagged off southwestern Australia.

methods. Only recaptures with data that included the date of recapture and accurate length at release and recapture were used in the analyses.

Gulland and Holt (1959) The first method used for estimating growth rates was that of constructing plots of growth rate by average fork length (Gulland and Holt, 1959). The average fork length was calculated as the average of the fork length at release and recapture. Von Bertalanffy growth parameters were estimated by fitting a line through the data. The slope of the line was equal to $-K$, and the intercept with the x-axis was equal to L_∞.

Fabens (1965) The Fabens (1965) method involved fitting the nonlinear function:

$$L_R = L + (L_\infty - L)\,(1 - e^{-Kd}), \qquad (1)$$

where L_R = the length at recapture;
L = the length at release; and
d = the period at liberty.

This function was fitted to the data by using the nonlinear estimation module in STATISTICA (Statsoft, 1998). The value of t_0 was estimated by solving the function for the value of T

$$L_T = L_0 + (L_\infty - L_0)\,(1 - e^{-KT}), \qquad (2)$$

where the value of L_0 = the mean size at birth; and
L_T = 0 cm.

The mean size at birth of *C. obscurus* from southwestern Australia was estimated by fitting a normal probability function to a size-frequency distribution of tagged individuals that had an open umbilical scar (Fig. 3). From these data the mean size at birth was 75.3 cm FL.

Francis (1988) method This method uses a maximum likelihood approach to fitting a growth function that includes estimated growth rates (g_α and g_β) at two selected lengths (α=75 cm FL and β=100 cm FL), the coefficient of variation of growth variability (v), measurement error (assumed to be normally distributed with a mean, m, and standard deviation, s), and outlier probability (p). The estimated growth increment for an individual, i, is given by

$$\Delta L_i = \left[\frac{\beta \cdot g_\alpha - \alpha \cdot g_\beta}{g_\alpha - g_\beta} - L_i\right]\left[1 - \left(1 + \frac{g_\alpha - g_\beta}{\alpha - \beta}\right)^{\Delta T_i}\right],$$

where L_i = the length at release; and
ΔT_i = the period at liberty.

Francis (1988) suggested several methods of incorporating growth variability into the model.

The likelihood function is

$$\lambda = \sum_i \log\left[(1-p)\lambda_i + p/R\right],$$

where $\lambda_i = \dfrac{\exp\left(-0.5(\Delta L_i - \mu_i - m)^2/(\sigma_i^2 + s^2)\right)}{\left[2\pi(\sigma_i^2 + s^2)\right]^{0.5}}$;

R = the range of the observed growth increments;

μ_i = the expected value of growth increment of the ith individual; and
σ_i = the standard deviation of the growth variability.

In the present study σ_i was assumed to be proportional to predicted growth increment (i.e. $\sigma_i = v\mu_i$).

The solver function in Microsoft Excel (Microsoft, 1999) was used to maximize the likelihood value of the model. Although the growth model allowed the use of six parameters, the number of parameters used for each of the groups was determined by using the likelihood ratio test (LRT). In its simplest form growth was assumed to be linear ($g_\alpha = g_\beta$) and to include s. The addition of more parameters (nonlinear growth [$g_\alpha \neq g_\beta$], v, m, and p) was significant if the likelihood increased by more than 1.92 per parameter (Francis, 1988). The final model used for each group was the one with the least number of significant parameters.

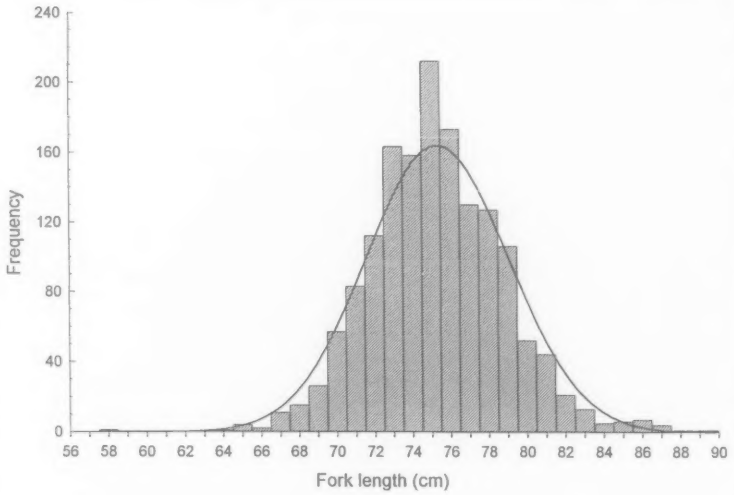

Figure 3

Size-frequency distribution of 1537 neonate *Carcharhinus obscurus* from southwestern Australia with open umbilical scars. The line represents a normal distribution with a mean of 75.3 cm and a standard deviation of 3.75 cm.

Bootstrapping was used to estimate 95% confidence intervals for parameter estimates. New growth increment values were generated by adding randomly selected points from two normal distributions. The first distribution had a mean of the predicted growth increment with a standard deviation equal to $v\mu$ and represented growth and growth variability. The second distribution represented the measurement error and had a mean of m and a standard deviation of s. Five hundred bootstrapped data sets were created by using each method and fitted by using the technique described above. Ninety-five percent confidence intervals were calculated from the 2.5th percentile and the 97.5th percentile of the resulting parameter distributions.

Length-at-age for neonate releases The use of length-at-age data is normally associated with aging studies where the age of an individual shark is estimated from the number of bands on the vertebrae. Because most animals tagged in the current study had open umbilical scars, it was possible to estimate the age of each of the recaptured animals directly from the time at liberty and the rate of healing of the umbilical scar. There is limited information available on the time that it takes for the umbilical scar to close, but most estimates range from 4 to 6 weeks (Bass et al., 1973). If it is assumed that a shark with an open scar was tagged at an age of three weeks (the assumed age at release), the age at recapture is the time at liberty plus three weeks. Preliminary data analysis showed that a linear growth function ($L_t = bL + a$, where b is the growth rate and a is a constant) provided a better fit to the data than a von Bertalanffy function. Thus a linear model was fitted to the length-at-age data. Growth rates (b values) were compared between males and females, and between injected and noninjected animals, using the homogeneity-of-slopes model within the visual general linear model module of STATISTICA. Significant differences in growth rates existed when the interaction term (age×sex or age×injection status) was significant. If there were significant differences in the growth rates for sexes then differences in the growth rates between injected and noninjected animals were assessed separately for males and females, otherwise they were assessed for males and females combined.

Results

A total of 473 recaptures of juvenile *C. obscurus* were reported to September 1998. Recaptured animals were at liberty between 0 and 1716 days (4.7 years); seven were at liberty for more than three years. Tag-recapture data from all individuals with usable data were included in the Francis (1988) method, whereas only those with times at liberty greater than 60 days were used in the other methods of analysis. Individuals at liberty less than 60 days were excluded because many individuals had growth rates that were beyond those considered reasonable because of the short period at liberty (Fig. 4). The size at recapture ranged from 68.5 to 147 cm FL. There were 304 recaptured sharks with usable data, and 274 recaptured sharks with times at liberty greater than 60 days. These recaptured sharks included 153 males (137 at liberty >60 days), 143 females (130 at liberty >60 days), 118 individuals injected

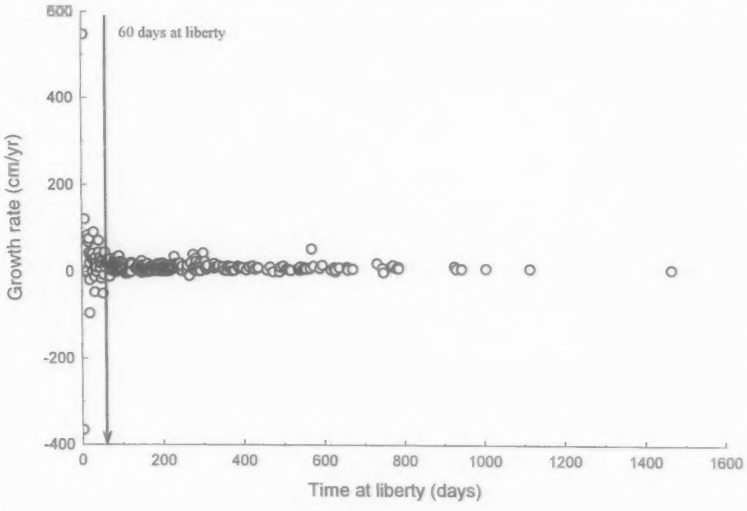

Figure 4

Growth rates of recaptured juvenile *Carcharhinus obscurus* from southwestern Australia as a function of time at liberty. The line indicates 60 days at liberty, the time below which individuals were excluded from analysis.

with OTC (111 at liberty >60 days), and 179 individuals not injected with OTC (160 at liberty >60 days).

Gulland and Holt (1959) method

Linear regressions fitted to the growth rate versus average fork length had positive slopes for all groups examined. As a result estimates of K were negative, and L_∞ was unsolvable. These results indicate that this method was unable to estimate growth parameters for juvenile *C. obscurus*.

Fabens (1965) method

Von Bertalanffy growth parameters estimated by the Fabens (1965) method varied widely (Table 1). All the groups, except the noninjected individuals, produced estimates of K between 0.092/year and 0.187/year, and estimates of L_∞ between 142 cm FL and 194 cm FL. For the noninjected individuals the estimate of K was 0.031/year and L_∞ was 379 cm FL. Values of r^2 for all groups were relatively high, indicating that the von Bertalanffy parameters explained most of the variation in the data.

Francis (1988) method

The likelihood ratio tests for each of the five groups of *C. obscurus* indicated that the appropriate models were relatively simple, containing linear growth (g_α=g_β), v, s, and sometimes m (Table 2). Contamination probability (p) and g_β were not included in the final models for any of the groups. The value of m was assumed to be zero for models in which it was not included.

Table 1

Estimates of von Bertalanffy growth parameters with the Fabens (1965) method for juvenile *Carcharhinus obscurus* from southwestern Australia.

Group	L_∞ (cm)	K (per year)	r^2
All	177	0.111	0.74
Male	195	0.092	0.80
Female	142	0.187	0.67
Injected	156	0.167	0.73
Noninjected	379	0.031	0.72

The Francis (1988) method estimated that the linear growth rate for all juvenile *C. obscurus* was 9.23 cm/year (Table 3). The growth rate of males was 1.1 cm/year higher than that for females, and 2.2 cm/year higher for OTC-injected than for noninjected animals. The 95% confidence intervals (CI), however, indicated that differences in growth rate were not significant between any of the five groups. Estimates of v and s were similar for all groups examined, ranging from 0.24 to 0.40 and from 2.09 cm FL to 2.54 cm FL, respectively. The 95% CIs indicated no significant differences in v or s between groups. The values of m, for models in which it was calculated, ranged from 0.69 cm FL to 0.94 cm FL. There were no significant differences in m between the all, females, and noninjected groups.

Table 2

Likelihood values from the Francis (1988) method for different combinations of parameters. Values in bold indicate the final model used in the analysis for each of the five groups of *Carcharhinus obscurus*. Significance of additional parameters was tested with the likelihood ratio test (see text for details).

Model	All	Male	Female	Injected	Noninjected
g_{75}, s	–807.23	–396.19	–386.90	–305.04	–470.90
g_{75}, v, s	–778.69	**–382.17**	–372.77	**–296.24**	–456.65
g_{75}, v, s, m	**–774.73**	–381.57	**–369.53**	–295.69	**–453.42**
g_{75}, v, s, m, p	–774.73	–381.57	–369.47	–295.69	–452.26
g_{75}, g_{100}, s	–806.76	–395.98	–386.81	–304.90	–497.58
g_{75}, g_{100}, v, s	–778.51	–382.16	–372.62	–295.83	–480.47
g_{75}, g_{100}, v, s, m	–774.69	–381.56	–369.46	–295.52	–476.73
g_{75}, g_{100}, v, s, m, p	–774.69	–381.56	–369.39	–295.52	–476.06

Table 3

Growth parameter estimates for five groups of *Carcharhinus obscurus* from southwestern Australia with the Francis (1988) method for the best models determined in Table 2. Numbers in parentheses after estimates are 95% confidence intervals calculated by bootstrapping.

Parameter	All	Male	Female	Injected	Noninjected
g_{75} (cm/year)	9.23	10.24	9.14	10.84	8.69
	(8.24–10.11)	(9.41–11.17)	(7.73–10.49)	(9.68–11.63)	(7.43–10.01)
v	0.34	0.34	0.33	0.24	0.40
	(0.26–0.42)	(0.24–0.43)	(0.21–0.45)	(0.23–0.37)	(0.28–0.52)
s	2.35	2.09	2.54	2.43	2.33
	(2.03–2.63)	(1.69–2.46)	(2.09–2.93)	(1.91–2.74)	(1.94–2.73)
m (cm)	0.69	—	0.94	—	0.83
	(0.22–1.17)		(0.23–1.67)		(0.12–1.49)

As a comparison to estimates of m and s from the Francis (1988) method, differences in the size at release and recapture for animals at liberty less than 30 days were determined. If it is assumed than these animals grew a negligible amount over this period, and the animals were measured perfectly by research staff at release, then the mean and standard deviation of the differences should provide an independent estimate of m and s. The mean difference in size for 38 *C. obscurus* at liberty less than 30 days was 1.17 cm FL, and the standard deviation was 2.09 cm FL (Fig. 5). These values are similar to those estimated from the model for most of the groups

Length-at-age for neonate releases

A total of 241 released neonates (with open umbilical scars) were recaptured, including 117 males, 120 females, four of unknown sex, 92 OTC-injected animals, and 149 noninjected animals. The linear growth rate based on all neonate recaptures was 9.4 cm/year. The growth rate was higher for males than for females, and higher for injected animals than for noninjected animals (Table 4). Comparison of growth rates with the homogeneity-of-slopes models (Fig. 6, Table 5) indicated that there were significant differences between males and females, and between injected and noninjected males. However, there was no significant difference between injected and noninjected females (Table 5).

Discussion

Shark growth studies have typically used the von Bertalanffy growth function to describe how sharks grow, including previous work on *C. obscurus* (e.g. Natanson et al., 1995; Natanson and Kohler, 1996). However, in the current study the results indicated that a linear growth curve more accurately describes the growth of juvenile *C. obscurus* up to five years of age. Pratt and Casey (1990) suggested that for some slow growing sharks (e.g. *Carcharhinus plumbeus*) a linear growth function might provide a better predictive model than the von Bertalanffy growth function. Although linear growth functions have been rarely used in fish growth studies, Bayliff (1988) reported that this type of function provided the best fit to

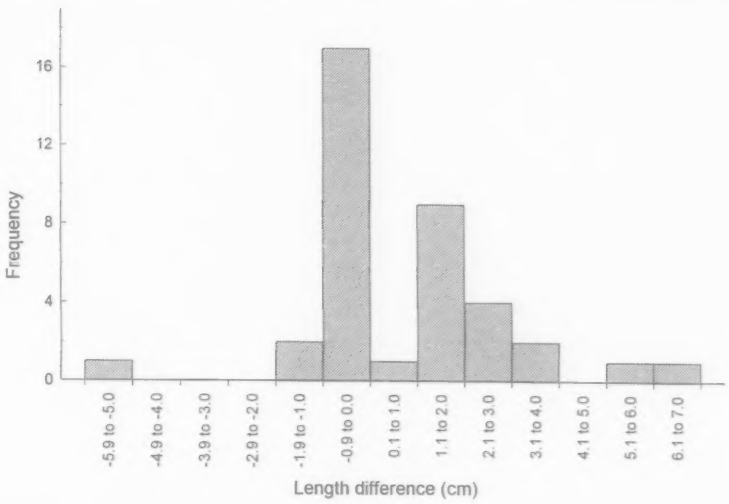

Figure 5

Differences between release and recapture lengths for 38 juvenile *Carcharhinus obscurus* at liberty less than 30 days off southwestern Australia.

growth data from tagged yellowfin tuna (*Thunnus albacares*) up to 100 cm long. Because the current study used only data from individuals up to five years old, which is a short period in relation to the estimated longevity of this species (45 years, Natanson et al., 1995), there was no information in the data on the rate at which the length reaches its asymptote (equivalent to the rate of decrease in the growth rate with increasing age). As a result the von Bertalanffy growth function cannot adequately describe the data. If recapture data were available for individuals from older age classes, it is likely that a decrease in growth rate with increasing age may have been observed and thus a von Bertalanffy growth function (or the Francis (1988) model with $g_\alpha \neq g_\beta$) may have provided the best fit to the data.

The Gulland and Holt (1959) method relies on a decrease in growth rates with increasing age to estimate both L_∞ (x-intercept) and K (slope). Thus, because the tag-recapture data for *C. obscurus* did not contain this information, the method was not able to estimate von Bertalanffy growth parameters. The inability to produce results, while other methods did, illustrates that the Gulland and Holt (1959) method fails in some situations where the periods at liberty are short in relation to the maximum age and where the recaptured individuals cover only a small proportion of the age classes present in the population. The lack of information in the data on the decrease in growth rate with increasing age also caused problems for the estimation of parameters in the Fabens (1965) method. In all cases, except for the noninjected group, this method provided substantially lower values of L_∞ than expected from observations of the maximum length of *C. obscurus* in Western Australian waters (280 cm FL, Simpfendorfer et al., unpubl. data[1]) and from previous growth studies (Natanson et al., 1995; Natanson and Kohler, 1996). Similarly, values of K were substantially higher than literature values (0.034 to 0.062, Natanson et al., 1995; 0.047, Natanson and Kohler, 1996) for each of the groups except the noninjected animals. The von Bertalanffy growth parameters estimated for the noninjected group by the Fabens (1965) method were similar to those estimated by Natanson et al. (1995) and Natanson and Kohler (1996).

Table 4

Linear growth rates (b) of juvenile *Carcharhinus obscurus* based on length-at-age data for neonate releases. Values in parentheses are standard errors of b.

Group	n	b (cm/yr)	r^2
All	241	9.39 (0.38)	0.706
Male	117	10.58 (0.48)	0.787
Female	120	8.46 (0.56)	0.644
Injected	92	10.05 (0.53)	0.773
Noninjected	149	8.54 (0.53)	0.633

[1] Simpfendorfer, C. A., R. McAuley, J. Chidlow, R. Lenanton, and N. Hall. 1999. Biology and stock assessment of Western Australia's commercially important shark species. Unpubl. report. Western Australian Marine Research Laboratories, PO Box 20, North Beach, Western Australia 6020, Australia.

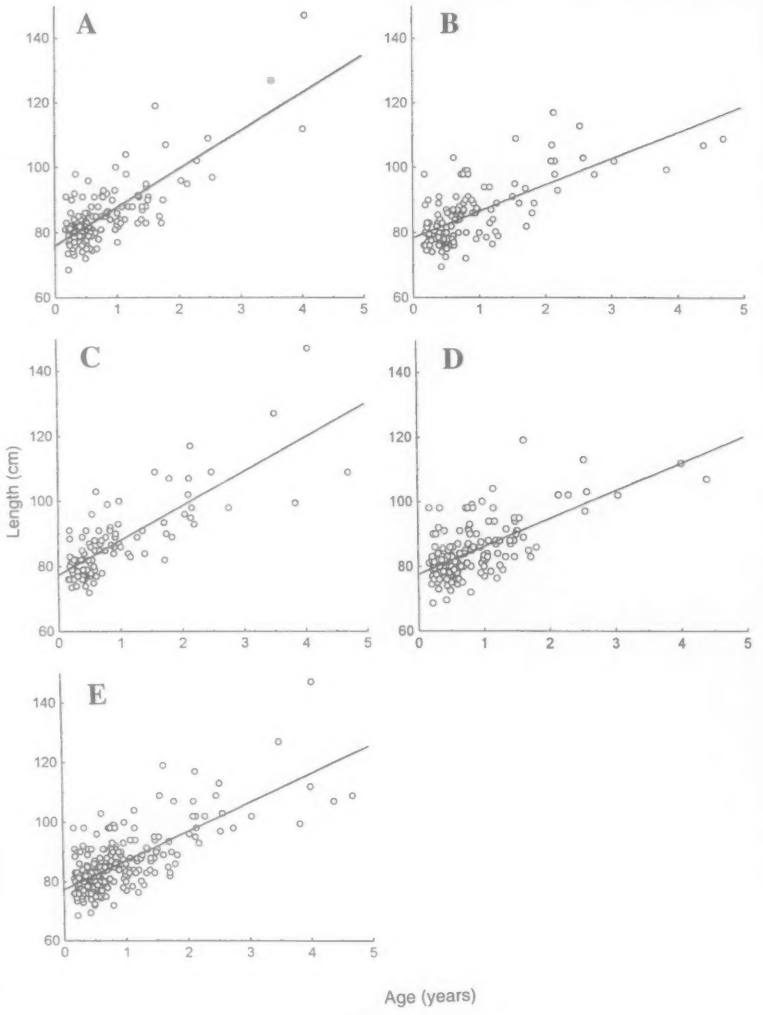

Figure 6

Length-at-age plots for (**A**) male, (**B**) female, (**C**) injected, (**D**) noninjected, and (**E**) all *Carcharhinus obscurus* from southwestern Australia. Lines represent linear growth functions based on parameters given in Table 4.

Despite the difficulties in obtaining von Bertalanffy growth parameters with the Fabens (1965) method, the growth rates from age zero to 5 years were similar to those from the linear growth function from the Francis (1988) and length-at-age methods (Fig. 7). Each of the methods indicates that on average juvenile *C. obscurus* grow 8–11 cm/year. The results from the current study (for all methods) were also similar to those from previous studies for *C. obscurus* in the western North Atlantic and southwestern Indian Ocean by Natanson et al. (1995) and Natanson and Kohler (1996), respectively (Fig. 7). However, the growth rates were lower than those suggested by Branstetter (1990) who used data from Schwartz (1983) to estimate the growth rate of *C. obscurus* pups from the western North Atlantic to be approximately 15 cm/year. At ages greater than five years, the growth rates estimated by the current study corresponded poorly to observed results in other studies. This is a result of the linear growth of the juveniles that does not predict the decrease of growth rates as individuals age. Extrapolation of the results to ages greater than five years is thus invalid and should be avoided.

The results of the Francis (1988) method indicate a relatively high level of growth variation in juvenile *C. obscu-*

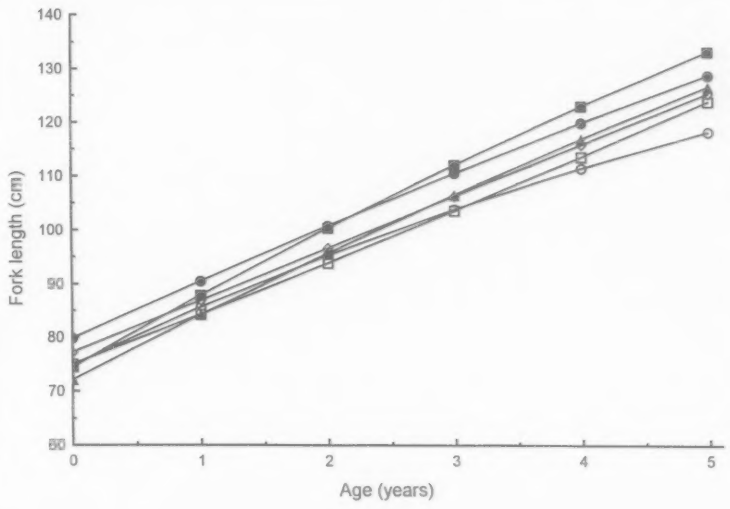

Figure 7

Comparison of growth rates from three methods used in the current study (open symbols: circle = Fabens [1965] method; square = Francis [1988] method; diamond = length-at-age method) and previous research (solid symbols: circle = length-at-age from vertebrae; square = tag-recapture data from Natanson et al. [1995]; triangle = Natanson and Kohler [1996]).

Table 5

Results of homogeneity-of-slopes models in which growth rates between male and female, and injected and noninjected *Carcharhinus obscurus* were compared. ** indicates significant effects. SS = sum of squares.

Comparison	Effect	SS	df	*F*	*P*
Male with female	sex	107.60	1	5.31	0.022**
	age	12997.64	1	641.44	0.000**
	sex × age	161.69	1	7.98	0.005**[1]
Male					
Injected with noninjected	injection status	7.72	1	2.99	0.086
	age	7012.62	1	555.84	0.000**
	injection status × age	224.323	1	17.78	0.000**
Female					
Injected with noninjected	injection status	18.02	1	0.68	0.411
	age	5720.07	1	216.34	0.000**
	injection status × age	0.34	1	0.013	0.910

[1] Because *age* × *sex* interaction is significant, comparisons of injected and noninjected groups must be conducted for males and females separately.

rus. The value of v in the present study (0.24–0.40) was higher than that estimated for *Galeorhinus galeus* (0.06) (Francis and Mulligan, 1998), but lower than for *Mustelus antarcticus* (0.58) (Francis and Francis, 1992). Francis and Mulligan (1998) suggested that their data might not contain enough information to distinguish between measurement error and growth variability. Francis (1997) and Francis et al. (1999) reported similar levels of growth variability for elephantfish (*Callorhinchus milii*) and hapuku (*Polyprion oxygeneios*), respectively. Growth variability therefore appears consistently to be relatively high across a range of elasmobranch, chimaerid, and teleost fishes.

The observed growth variability in juvenile *C. obscurus* may in part have been due to seasonal growth variation, migrations between warmer waters on the west coast of Western Australia, and cooler waters on the south coast. Either of these factors could possibly have produced substantial variation in growth rates. Further research on the influence of temperature on growth of *C. obscurus* would prove useful in isolating the causes of growth variability in this species.

The estimated measurement error parameters from the Francis (1988) method were similar but slightly lower than those from the differences in length for individuals at liberty less than 30 days. The close agreement between these results indicates that the Francis (1988) method provides accurate estimates of measurement error and that the confounding of measurement error and growth variability reported by Francis and Mulligan (1998) was not a problem in the current study. The magnitude of the mean measurement error was small (0–0.94 cm) in relation to the length of the sharks examined (55–140 cm). Previous studies using the Francis (1988) method have indicated that including m in the model does not improve the result, whereas values of s have included 1.2 cm (*C. milii*, Francis, 1997), 1.5 cm (*P. oxygeneios*, Francis et al., 1999), 1.6 cm (*Mustelus lenticulatus*, Francis and Francis, 1992) and 7.2 cm (*G. galeus*, Francis and Mulligan, 1998).

The length-at-age analysis indicated that male juvenile *C. obscurus* have significantly higher growth rates than females. This result, however, was not supported by the results from the Francis (1988) method that showed overlap in the 95% confidence intervals derived from bootstrapping. Differences in growth rates do occur between the sexes in sharks, but these differences are most commonly observed at ages close to maturity (approximately 20 years in *C. obscurus*) (e.g. Simpfendorfer, 1993; Simpfendorfer et al., 2000). Thus the lack of significant differences in the growth rate between young male and female *C. obscurus* was not unexpected. The difference in the results between the two methods may be due to the simple linear model fitted to the length-at-age data not being able to account for growth variability and measurement error. This demonstrates the improvement in understanding that the more complex Francis (1988) model can provide over more simplistic approaches.

The results of the length-at-age analysis in the current study indicate that male *C. obscurus* injected with OTC have significantly higher growth rates than noninjected males. However, females showed no significant difference between injection and noninjection with OTC. The parameter estimates from the Francis (1988) model indicated that injected animals grow 2.2 cm/year faster than noninjected animals. However the 95% confidence intervals overlapped slightly (injected, 9.68–11.63; noninjected, 7.43–10.01) indicating that there were no significant differences in growth rates. Although the significance of growth rate differences varied between analysis methods and sexes, suggesting that differences may have been the result of biased data, there is sufficient evidence to warrant further investigation of the effect of OTC injection on juvenile *C. obscurus*. Previous studies of elasmobranchs have not found significant differences in growth rates between injected and noninjected animals (Tanaka, 1990; Gelsleichter et al., 1998; Natanson et al., 1999). However, only one of these studies (Natanson et al., 1999) was carried out on sharks in the wild. This study was based on four OTC-injected *G. cuvier* specimens and no statistical comparison of growth rates between injected and noninjected individuals was undertaken.

If growth differences between OTC-injected and noninjected *C. obscurus* do occur, they may result from the antibiotic properties of OTC. It is likely that injections of OTC would not increase growth rates; rather, the growth of noninjected animals may be lower after tagging. The capture and tagging process is likely to present a significant source of stress for sharks—one that may increase their chances of microbial infection and slow their growth (e.g. Olsen, 1953; Davies and Joubert, 1967; Manire and Gruber, 1991). Animals injected with OTC would be more likely to overcome these infections quickly and thus grow at rates indicative of untagged individuals. If this scenario can be proven, then the faster growth rates predicted by the Francis (1988) method for the injected juvenile *C. obscurus* (10.84 cm/year) are likely to be most representative for this species.

This study indicates that although a range of techniques are available to estimate growth rates and von Bertalanffy growth parameters from tag-recapture data, they can produce variable results. One method, the Gulland and Holt (1959) method, was not able to produce results for juvenile *C. obscurus*. Another, the Fabens (1965) method, produced unrealistic von Bertalanffy growth parameters. Two methods, the Francis (1988) and length-at-age methods, indicated that linear growth functions provided better predictive power for juvenile *C. obscurus* than the nonlinear von Bertalanffy growth function. The use of the Francis (1988) method allowed for a more detailed investigation of the growth of *C. obscurus*, including the investigation of measurement error and growth variability. Estimation of these additional parameters is particularly useful in tag-recapture studies where commercial and recreational fishermen provide the majority of data. Thus, although the more traditional methods are still commonly used for elasmobranchs, researchers should consider the use of more detailed approaches, such as that of Francis (1988), to extract the maximum possible information from their data.

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Effects of year and region on the abundance and size of age-0 walleye pollock, *Theragra chalcogramma*, in the western Gulf of Alaska, 1985–1988*

Matthew T. Wilson

Alaska Fisheries Science Center
National Marine Fisheries Service, NOAA
7600 Sand Point Way NE
Seattle, Washington 98115
E-mail address: matt.wilson@noaa.gov

Abstract–Effects of year and region on young-of-the-year (age-0) walleye pollock abundance and size were examined by using bottom and midwater trawl collections made during 1985–88. Samples were collected from shelf and coastal areas in three adjacent regions of the western Gulf of Alaska. The primary focus was to examine regional differences in recruitment prediction and annual differences in fish distribution. Fish density was used to indicate abundance, and length was included as a relevant factor in fish production. Year and region significantly interacted as effects on age-0 density. Recruitment prediction was best in the Kodiak Island region, upstream of the main spawning area, where fish densities were high during 1985 and 1988 in relation to 1986 and 1987. On a large scale, fish were evenly distributed every year, except during 1987 when their density increased strongly from east to west. Age-0 length also varied with year and region. This was apparent after accounting for daily increases in mean length (0.09 cm/d). Fish were comparatively small during 1986, intermediate during 1985, and large during 1987 and 1988. Regional differences in fish length were due to a relative abundance of large-size fish around Kodiak Island where the average size was about 0.75 cm larger than elsewhere. Thus, a relative abundance of large individuals in this region was associated with good recruitment prediction. These results are discussed in terms of their relevance to spatial variation in the production of recruits.

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Young-of-the-year (age-0) fish abundance is used in managing temperate marine resources (Goodyear, 1985; Bailey et al., 1986; Johannessen and Tveite, 1989; Sundby et al., 1989; Galaktionov, 1993; Corten[1]). Estimating the abundance of age-0 fish, however, is complicated by their broad and sometimes variable spatial distributions. This variability, which can obscure shifts in distribution from changes in abundance (Olsen and Soldal, 1989; de LaFontaine et al., 1992; Polacheck et al., 1992; Anderson et al., 1995), may affect survival.

Walleye pollock, *Theragra chalcogramma*, are semidemersal gadids that reside in the North Pacific Ocean (Lynde, 1984; Springer, 1992; Wolotira et al., 1993). The National Oceanic and Atmospheric Administration (NOAA) has sought to understand and predict pollock recruitment better because of the commercial importance and recruitment variability of the species (Kendall and Duker, 1998; Hollowed et al.[2]; Wespestad et al.[3]). Much of the research on pollock recruitment has been done in the western Gulf of Alaska (GOA) as part of NOAA's Fisheries Oceanography Coordinated Investigations (FOCI) program (Schumacher and Kendall, 1991; Kendall et al., 1996).

In the GOA, many pollock spawn during early April in southwestern Shelikof Strait (Picquelle and Megrey, 1993) (Fig. 1). This spawning is believed to be primarily responsible for replenishing the GOA pollock stock (Kendall and Picquelle, 1990; Hollowed et al.[2]). FOCI researchers have devised a transport paradigm for young pollock of Shelikof Strait, in which they move with the prevailing currents from the main spawning area in the Strait to shelf and coastal nurseries farther southwest (Schumacher and Kendall, 1995; Kendall et al., 1996). Although some individuals may be carried beyond the shelf, the oceanic North Pacific is not considered an important pollock nursery area (Smith et al., 1984). This pattern of dispersal, hereafter referred to as the FOCI recruit-pathway paradigm, was demonstrated in 1987 (Hinckley et al., 1991), and it has been simulated by a model of larval transport that incorporates detailed physical and biological information (Hermann et al., 1996a,

* Contribution 0262 of the Fisheries Oceanography Coordinated Investigations, 7600 Sand Point Way, NE, Seattle, WA 98115.

[1] Corten, A. 1986. Application of the results from international young fish surveys in fisheries management in recent years. ICES, Doc. C.M. 1986/G:54, 26 p.

[2] Hollowed, A. B., E. Brown, J. Ianelli, P. Livingston, B. Megrey, and C. Wilson. 1997. Walleye pollock. *In* Stock assessment and fishery evaluation report for the groundfish resources of the Gulf of Alaska, p. 31–119. Prepared by the Gulf of Alaska Groundfish Plan Team, North Pacific Fishery Management Council, P.O. Box 103136, Anchorage, AK 99510.

[3] Wespestad, V. G., J. N. Ianelli, L. Fritz, T. Honkalehto, N. Williamson, and G. Walters. 1997. Bering Sea-Aleutian Islands walleye pollock assessment for 1998. *In* Stock assessment and fishery evaluation report for the groundfish resources of the Bering Sea/Aleutian Islands regions, p. 35–102. Prepared by the Bering Sea/Aleutian Islands Plan Team, North Pacific Fishery Management Council, P.O. Box 103136, Anchorage, AK 99510.

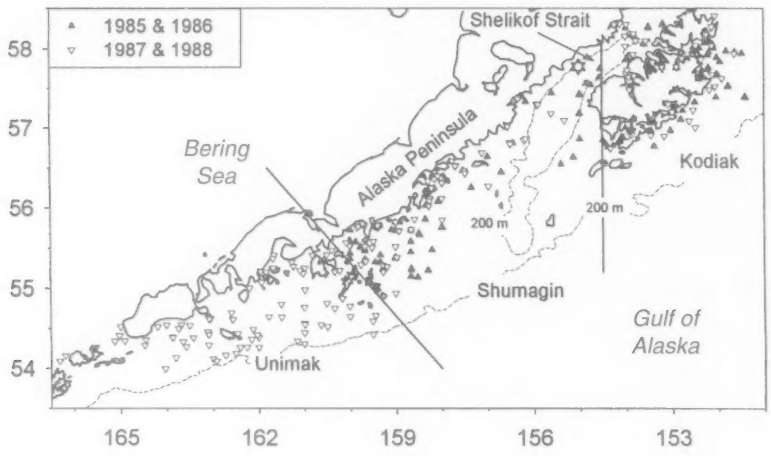

Figure 1

Map of the NMFS exploratory sampling locations for age-0 pollock in the western Gulf of Alaska, August–October, 1985–88. The straight lines delineate the three regions used to group the data geographically. The star (☆), near the head of the arrow pointing to Shelikof Strait, marks the major pollock spawning area.

1996b). Consequently, the shelf area west of Shelikof Strait has received the most attention recently regarding pollock nurseries in the western GOA (Brodeur et al., 1995; Wilson et al., 1996).

Not all observed distributions of age-0 pollock, however, are consistent with the FOCI recruit-pathway paradigm. In 1980–82, some incidental collections of age-0 pollock were made during bottom trawls for shrimp in bays throughout the western GOA. High age-0 densities were found northeast of the main spawning area and led Smith et al. (1984) to conclude that important spawning areas probably exist farther upstream. Small concentrations of pollock eggs, larvae (Kendall and Picquelle, 1990; Dunn et al.[1]), and spawning adults have been found throughout the western GOA (Hirschberger and Smith, 1983; Hollowed et al.[2]; Williamson[5]; Karp[6]; Wilson et al.[7]). This does not, however, preclude the possibility that dispersal of young from Shelikof Strait is more variable than previously thought.

In response to conclusions drawn by Smith et al. (1984), the National Marine Fisheries Service (NMFS) conducted more spatially extensive surveys designed to map age-0 abundance and size (Spring and Bailey[8]). These surveys occurred during 1985–88. The data were included in a compilation of information by Bailey and Spring (1992) primarily to show that year-class strength was set by the age-0 stage. Like Smith et al. (1984), however, Bailey and Spring also found that many juveniles were present in the Kodiak region during some years.

This study presents a re-examination of the 1985–88 survey data. In this study, however, the effects of year and region were evaluated statistically and length was included due to its relevance to recruitment. Among juvenile fish, size often has a positive effect on survival (Sogard, 1997; Hurst and Conover, 1998; Schultz et al., 1998). Emphasis was placed on annual variability within each of three regions owing to interest in developing a recruitment predictor. Emphasis was also placed on within-year regional variability because of the possibility

[1] Dunn, J. R., A. W. Kendall Jr., R. J. Wolotira Jr., J. H. Bowerman Jr., D. B. Dey, A. C. Materese, and J. E. Munk. 1980. Seasonal composition and food web relationships of marine organisms in the nearshore zone—including components of the ichthyoplankton, meroplankton, and holoplankton. Final Report OCSEAP RU551. Northwest and Alaska Fisheries Center, Natl. Mar. Fish. Serv., NOAA, 2725 Montlake Blvd. E., Seattle, WA 98112, 393 p.

[5] Williamson, N. J. 1989. Acoustic-midwater trawl surveys for walleye pollock in the Gulf of Alaska in 1989. *In* Condition of groundfish resources of the Gulf of Alaska in 1989 (T. K. Wilderbuer, ed.), p. 281–311. U.S. Dep. Commer., Alaska Fisheries Science Center, 7600 Sand Point Way NE, Seattle, WA 98115.

[6] Karp, W. A. 1990. Results of echo integration midwater-trawl surveys for walleye pollock in the Gulf of Alaska in 1990. *In* Stock assessment and fishery evaluation report for the 1991 Gulf of Alaska groundfish fishery, Appendix 3, 42 p. Prepared by the Gulf of Alaska Groundfish Plan Team, North Pacific Fishery Management Council, P.O. Box 103136, Anchorage, AK 99510.

[7] Wilson C., M. Guttormsen, and S. K. de Blois. 1996. Echo integration-trawl survey results for pollock in the Gulf of Alaska during 1996. *In* Stock assessment and fishery evaluation report for the groundfish resources of the Gulf of Alaska, p. 417–443. Prepared by the Gulf of Alaska Groundfish Plan Team, North Pacific Fishery Management Council, P.O. Box 103136, Anchorage, AK 99510.

[8] Spring, S., and K. Bailey. 1991. Distribution and abundance of juvenile pollock from historical shrimp trawl surveys in the western Gulf of Alaska. U.S. Dep. Commer., NOAA Proc. Rep. AFSC 91-18, 66 p.

that the Kodiak region is sometimes a relatively important nursery area despite its position upstream of the main spawning area.

Materials and methods

The data selected for this study comprise the longest time series available from the GOA where the collection method was consistent (Bailey and Spring, 1992; Spring and Bailey[8]). They were collected in late summer (August–October) 1985–88 by the NMFS (Fig. 1, Table 1). The purpose of these surveys was to obtain a coarse picture of the distribution and size of age-0 pollock in the western GOA; These surveys were the first to target age-0 pollock in this area and, as such, were exploratory.

The area surveyed was the continental shelf and bays around Kodiak Island and as far southwest as time allowed (Fig. 1). The Alaska Coastal Current (ACC) flows southwestward through the area but circulation is complicated by sea valleys, islands, and other topographic complexity (Lagerloef, 1983; Reed and Schumacher, 1986; Stabeno et al., 1995). The largest sea valley forms Shelikof Strait and it forms a natural division within the western GOA between eastern and western regions. The Kodiak Island Archipelago is a prominent feature of the eastern region. Smaller islands characterize the western region, which has a relatively broad shelf.

Sampling was accomplished by trawling on echo layers. Echo sign was monitored along predetermined transects. No effort was made to include acoustic data because a preliminary study found no relation between echo sign and age-0 catches (Bailey and Spring, 1992). Samples were collected only during the day, so that the problem of diel vertical fish migration was avoided.

Echo sign believed to be age-0 pollock was sampled by using an 18.6-m high, opening shrimp trawl with steel V-doors (1.5 m × 2.1 m, 568 kg) attached by 18-m bridles. The trawl was made of 3.2-cm stretched-mesh, nylon netting, and a 3-mm mesh liner was inserted into the codend. For bottom samples, a 16.8-m tickler chain was used and the footrope of the net was held above a bottom contact chain by 30-cm chain lengths. For midwater tows, a 363-kg weight was attached to each lower wing to help hold the trawl mouth open, and the chain on the footrope was removed. A netsonde system (BEN-MAR or Furuno) was used to position the trawl vertically at the desired depth. It was not possible to open and close the net at depth. Towing speed and duration averaged about 4.5 km per h and 10–15 min, respectively. At each sampling location, sea surface temperature was measured with a bucket thermometer.

All taxa caught were identified, enumerated, and weighed. At this time of year, age-0 pollock are readily distinguished from older individuals by a clear separation in size (Bailey et al., 1996b; Brodeur and Wilson, 1996a; author's unpubl. data). Fork length was measured to the nearest centimeter. All age-0 pollock were measured except those in large catches, when about 100 randomly selected fish were measured. Length data were missing for five samples, each of which comprised only a few fish.

Table 1

Dates and number of tows made during the 1985–88 NMFS surveys of age-0 pollock in the western Gulf of Alaska. The estimated Gulf-wide abundance for each year class at age-2 from Bailey et al. (1996a) is included as an index of recruitment.

Year	Dates sampled	Number of tows	Recruitment ($\times 10^9$)
1985	21 Aug–10 Sep	113	1.43
1986	3 Sep–9 Oct	95	0.22
1987	12 Aug–20 Sep	118	0.30
1988	18 Aug–10 Sep	80	2.16

The effect of year and region was examined first on age-0 abundance, and then on age-0 length. Finally, year- and region-specific abundance and size estimates were compared with recruitment.

Examination of effects of year and region on age-0 abundance was accomplished in five steps. The first step was to standardize the catch to account for differences in the volume filtered between tows. Volume filtered for each tow was calculated as the trawl mouth area times distance fished. The mouth area was assumed to be 37 m^2 for hauls on the bottom (Wathne, 1977) or 28 m^2 for hauls in midwater (Wilson et al., 1996). No adjustment was made for differences in the depth sampled because most (92%) samples were collected at depths where net dimensions are relatively stable (Wilson et al., 1996). Distance fished was the straight-line distance between two geographic points along which the net was fished at depth. Dividing each age-0 catch by the volume filtered produced fish density (fish per m^3), which was used to indicate abundance. Volume was not converted to sea surface area because of uncertainty about the depth and area represented by each sample. By using density, the assumption of a constant depth and area is explicit, and different values can easily be applied *post-hoc* if an estimate of absolute abundance is desired.

The second step was to adjust for mortality during the 3–5 week survey period. An instantaneous daily mortality rate of 0.014 (Hollowed et al., 1996) was used to adjust each density to the overall median survey date (3 September).

The third step was to account for 22 tows throughout the survey area that were apparently replicates of other tows. Samples were judged to be pseudoreplicates if they were consecutive, were the same type (bottom or midwater), and were within one nautical mile and 50 m depth of each other. The pseudoreplicates were averaged together to give 384 samples from the original 406 trawl hauls.

The fourth step was to group fish densities by geographic area by using the three regions defined by Bailey and Spring (1992). A minor adjustment to this stratification scheme involved moving the delineation between the Unimak and Shumagin regions farther west to better reflect annual differences in sampling effort (Fig. 1). The Unimak Island region was surveyed only during 1987–88. Thus, samples from the area upstream of the main spawn-

ing site were separated from samples collected farther downstream, and the difference in large-scale coverage was accommodated.

Finally, statistical tests were conducted to examine effects of year and region on age-0 density, which was not straightforward owing to the occurrence of many zeros and a few very large values in the catch data. Four different procedures were employed and the results were compared. All statistical tests were accomplished with SYSTAT for Windows (Wilkinson, 1996).

The first procedure was a two-way analysis of variance (ANOVA) of two different transformations of all four years of data. One ANOVA was based on a log-transformation (Sparholt et al., 1991) ($\log_{10}$(density)+0.00001, nonzero catches ranged from 0.00001–0.6 fish per m^3) and the other was based on rank-transformed data (Conover, 1980). Neither transformation, however, removed the spike of zeros in the frequency histogram of densities and thus made the requisite assumption of normality tenuous. To avoid empty cells data from the Unimak region were omitted; they were collected only during 1987–88.

The second procedure was a distribution-free, nonparametric test to again look for effects of year and region (Methven and Bajdik, 1994). Unlike Methven and Bajdik (1994), however, the age-0 data were not paired; therefore the signed rank test was replaced by the Kruskal-Wallis test. Because this is a one-way test, subsets of the data were selected so that the effect of the first factor was examined within a level of the second factor (e.g. year within a region) and *vice-versa* (e.g. region within a year) (Valle et al., 1999). In all, seven tests were run. Significance of the outcome for each test was based on the Bonferroni-corrected alpha level of 0.05.

The third and fourth procedures were conducted primarily as a means to circumvent the zero-catch problem but also because of differences in the information conveyed by zero and nonzero catches (Pennington, 1983; Randa, 1984). Zero catches indicate absence, and nonzero catches indicate presence as well as some measure of abundance.

The third procedure involved chi-square tests to test whether the presence or absence of age-0 pollock was associated with year or region. Annual or regional differences in age-0 frequency of occurrence indicate a change in fish patchiness, or a change in the ability to target them; both may be associated with a change in abundance. It was necessary to conduct one chi-square test for each region to examine annual differences and then for each year to examine regional differences. Thus, Bonferroni corrections were again necessary.

The fourth procedure was a two-way ANOVA test of effects of region and year on nonzero densities. The nonzero densities appeared normally distributed after being $\log_{10}$-transformed. Again, the Unimak data were omitted.

A year-region interaction term was included in the ANOVA tests of the first and fourth procedures. Significance of the interaction term indicates that annual differences vary by region, or that regional differences vary by year. The former identifies regions with high annual variability; whereas the latter implies annual variation in fish distribution. Significance of the interaction term determined which multiple comparison test was used *post hoc*. If it was not significant, a Bonferroni multiple comparison test was used for comparing levels of significant main effects. If it was significant, Fisher's least significant difference (LSD) test was preferred. In SYSTAT, the LSD test does not automatically correct for the number of comparisons being made (Wilkinson, 1996). This correction was desirable because only a subset of all possible pair-wise comparisons was of interest. Only comparisons among regions within year and among years within region were of interest, those involving different years and regions (i.e. 1985 Kodiak versus 1986 Shumagin) were excluded. A Bonferroni correction was then applied to the remaining comparisons to maintain an overall 0.05 alpha level.

Examination of effects of year and region on age-0 length was accomplished by using a two-way analysis of covariance (ANCOVA). An ANCOVA was necessary to account for variation in length due to differences in the collection day-of-year (expressed as the number of days since 1 January). The first ANCOVA was used to examine data collected from the Kodiak and Shumagin regions during all four years. The second ANCOVA was conducted with just the 1987 and 1988 data to compare lengths among all three regions. The covariate was not allowed to interact with the main effects (ie. slope homogeneity was assumed rather than tested) owing to the short duration of collecting in some regions and years in relation to the variation in mean length per haul. As in Anderson et al. (1995), the dependant variable was mean length per haul rather than individual length measurements; this variable simplified the model but allowed no within-haul variability. Mean size was weighted by mortality-adjusted fish density.

The relationship between annual estimates of age-0 density or size and recruitment was examined graphically because there were insufficient degrees of freedom for a global significance test of correlation. Pollock recruitment was indicated by the Gulf-wide abundance of age-2 individuals (Bailey et al., 1996a). No attempt was made to account for autocorrelation in this time series because pollock exhibit low autocorrelation in recruitment (Hollowed et al., 1998).

Results

Overall, 406 trawl samples were collected yielding 384 density estimates (zero and nonzero catches) and 335 estimates of mean length (Table 2). Stations were occupied from west to east, except in 1985 when sampling progressed from east to west and then doubled back to end near northeast Kodiak Island. Sampling around Kodiak Island was mostly over the inner shelf and in bays (Fig. 1). Coverage of the outer shelf was best farther west, between 158° and 164°W longitude. Sample depth varied considerably, and it appears that the daytime vertical position of age-0 pollock was also quite variable (Fig. 2).

Abundance

Results from each of the four statistical procedures consistently indicated that year and region interact in their

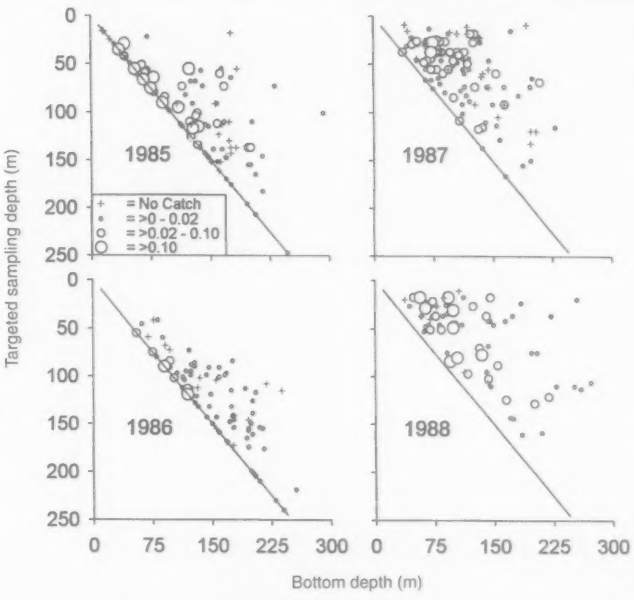

Figure 2

The vertical distribution of age-0 pollock density in the western Gulf of Alaska, August–October, 1985–88. Symbol size indicates the mortality-adjusted number of fish/m^3. The diagonal line indicates bottom depth.

effect on age-0 density. Annual differences were always limited to the Kodiak region where fish densities were high during 1985 and 1988 in relation to 1986 and 1987 (Table 2). Within other regions, annual differences were not significant. As to within-year patterns, regional differences were mostly limited to 1987 when fish density increased strongly from east to west (Fig. 3, Table 2). The distribution in each other year was more even. For brevity, only results from the first statistical procedure are tabulated.

In the first procedure, significant year-region interaction was indicated by each two-way ANOVA of transformed fish densities (Table 3). Fisher's LSD test indicated annual differences only in the Kodiak region (Table 4), where age-0 density was relatively high during 1985 and 1988 (Table 2). The LSD test also indicated regional differences, but only during 1987 or 1988, depending upon transformation (Table 4). When log-transformed, the regional effect was associated with low age-0 densities in the Kodiak region during 1987. When rank-transformed, it was associated with high densities in the same region but during 1988. The Unimak region was excluded from these tests.

In the second procedure, only two of the seven Kruskal-Wallis tests rejected the null hypothesis of equal fish densities. The first indicated an annual effect within the Kodiak region (Kruskal-Wallis test statistic=25.31, $P<<0.0001$). The second indicated a regional effect within 1987, which included the Unimak region (Kruskal-Wallis test statistic=32.24, $P<<0.0001$).

In the third procedure, only one chi-square test outcome was significant (chi-square=15.19, $P=0.0005$). During 1987, the frequency of occurrence around Kodiak Island was low (65%) in relation to occurrences in the Unimak region (98%) (Table 2).

In the fourth procedure, the two-way ANOVA of nonzero densities revealed a significant year-region interaction (df=3,241, $F=4.462$, $P=0.005$). Fisher's LSD test indicated that all differences occurred within the Kodiak region where nonzero density was relatively high during 1985 and 1988 (Table 2).

Length

Overall, 35,530 age-0 pollock were measured. They were collected from 335 trawl hauls and ranged from 3 to 13 cm FL. Significant effects of year and region were detected after accounting for a day-of-year effect (Table 5).

Daily increases in mean length per haul averaged 0.090 cm (Fig. 4), which is within the range of published growth rates for these fish (0.6–1.2 mm/d) (Bailey et al., 1996b). Two samples had unusually low mean length per haul (in 1986 and 1987) and were from bays; these represented few fish and so had little effect on the fitted lines.

Annual differences in length were due to a comparatively small mean size during 1986, a medium size during 1985, and large sizes during 1987 and 1988 (Fig. 4, Table 2). A Bonferroni multiple comparison test indicated that 1985 and

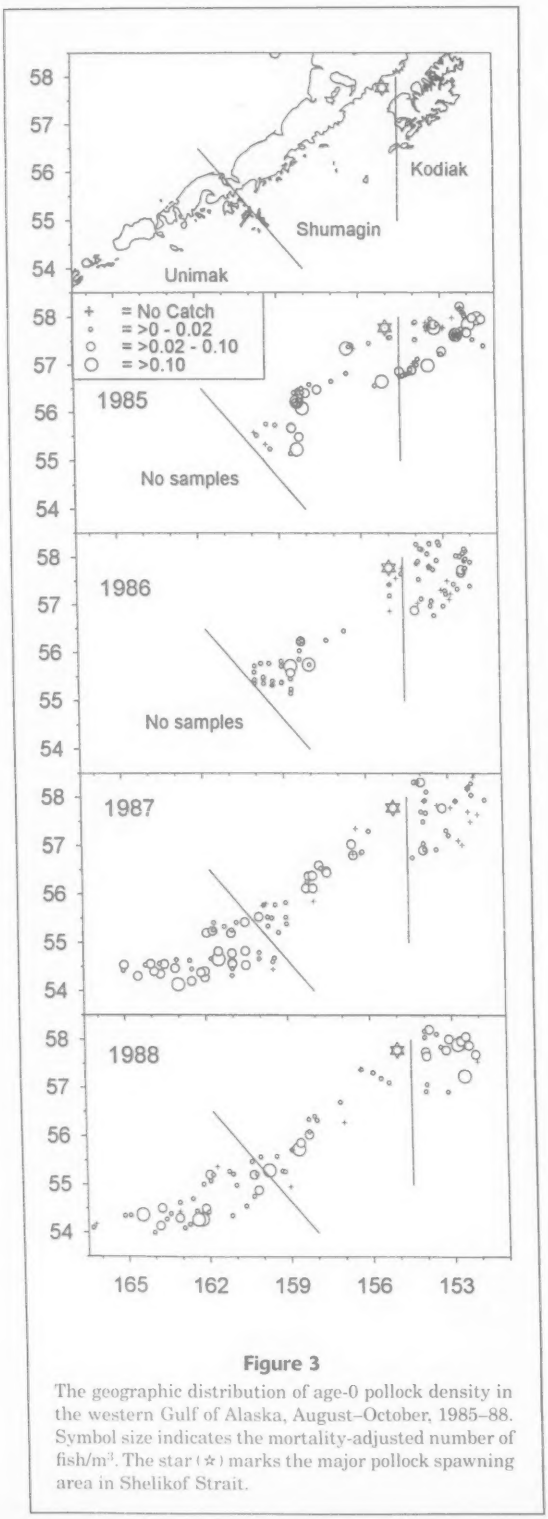

Figure 3

The geographic distribution of age-0 pollock density in the western Gulf of Alaska, August–October, 1985–88. Symbol size indicates the mortality-adjusted number of fish/m^3. The star (☆) marks the major pollock spawning area in Shelikof Strait.

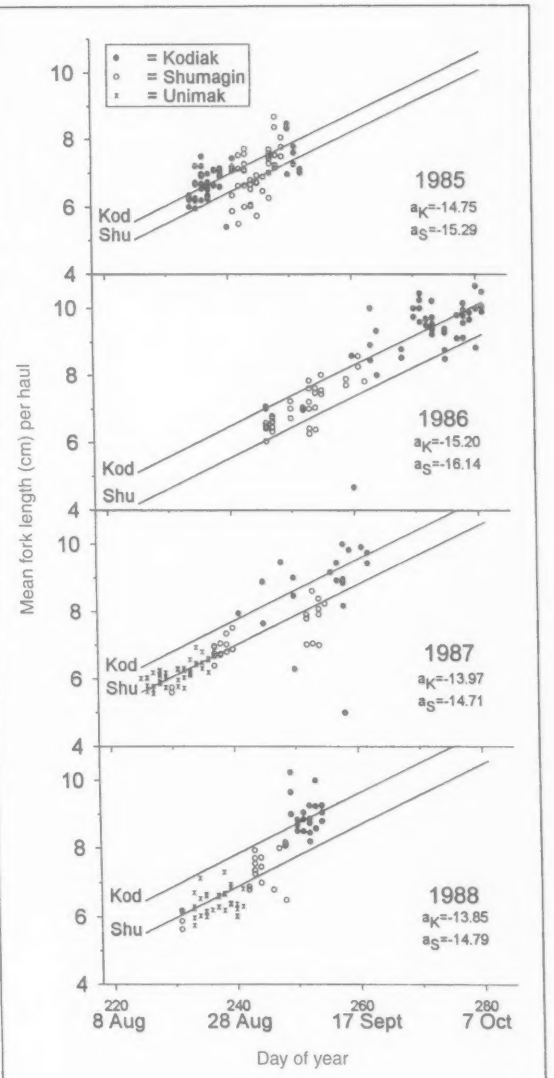

Figure 4

Age-0 pollock mean fork length per haul versus collection date for each year sampled August–October, 1985–88. Symbol type indicates region (see Fig. 1). Lines represent the least-squares linear fit from the ANCOVA of Kodiak and Shumagin data (slope=0.090; intercepts, a_K and a_S, respectively, are given)

1986 were each significantly (P<0.05) different from all other years. The year-region interaction term was marginally not significant (Table 5). A noteworthy correspondence between mean size and water temperature is apparent in Table 2.

Regional differences were due to a relative abundance of large-size fish in the Kodiak region. These fish were on average about 0.5–1.0 cm larger than the fish from elsewhere

Table 2

Catch and sample statistics, by region and year, for age-0 pollock collected in the western Gulf of Alaska during 1985–88. Mean $\log_{10}$, mean fork length (FL), mean sample depth, and mean sea-surface temperature were based on samples where age-0 pollock were caught. As stated in the text, fish density and length were adjusted to the median survey date (3 Sept) to account for differences in collection date. (Freq. occur.=frequency of occurrence).

Year class	Region	Total sample number	Freq. occur. (%)	Mean $\log_{10}$ (fish/m^3)	Mean (fish/m^3)	Median (fish/m^3)	Mean FL (cm)	Mean depth (m)	Mean temp. (°C)
1985	Kodiak	62	77	−2.19	0.0303	0.0038	7.5	101	10.5
	Shumagin	41	90	−2.19	0.0496	0.0073	6.9	88	10.9
1986	Kodiak	52	83	−2.84	0.0060	0.0008	7.0	136	9.3
	Shumagin	40	88	−2.74	0.0147	0.0015	6.1	116	10.8
1987	Kodiak	37	65	−3.06	0.0046	0.0001	8.2	75	11.2
	Shumagin	29	83	−2.32	0.0180	0.0053	7.5	70	11.6
	Unimak	44	98	−1.86	0.0302	0.0264	7.6	40	11.2
1988	Kodiak	20	95	−1.76	0.0544	0.0225	8.4	95	10.8
	Shumagin	23	83	−2.59	0.0242	0.0024	7.4	64	11.7
	Unimak	36	92	−2.12	0.0263	0.0063	7.7	35	11.0

(Table 2). The data from 1985 clearly show how the Kodiak and Shumagin regions contrast in terms of fish size (Fig. 4). Note that the difference in mean size coincides roughly with regional delineation. On closer inspection, it was apparent that large fish tended to concentrate near the northeast- and east-side of Kodiak Island in 1985 and 1988. Thus, size variability appears to also exist on a finer geographic scale. In Figure 4, most mean lengths from the Shumagin region in 1986 are above their respective line because one sample of relatively small fish accounted for almost 30% of the total density. During 1987 and 1988, means from the Unimak region were not different from those in the Shumagin region (Bonferroni, P=0.054) but they were different from the Kodiak group (Bonferroni, P=0.003). This difference was indicated by a second ANCOVA, and a second *post-hoc* multiple comparison test, wherein day (df=1 and 156, F=196, P<0.001) and region (df=2 and 157, F=22, P<0.001) were the only significant effects.

To address a possible association between regional mean size and mean sample depth (Table 2), the ANCOVA of 1985–88 data was rerun with sample depth as a third effect. Sample depth was included as a categorical effect with two levels: 50–100 and 100–150 m. Only 174 mean length estimates were used because the number of estimates at other depths was low or zero in some regions and years. Results were similar to the first run and there was no significant depth effect. Depth was neither significant by itself (df=1 and 157, F=0.118, P=0.731) nor did it interact with other effects (P>0.05). The difference in fish size between the Kodiak and Shumagin regions was therefore not likely due to differences in sampling depths.

Recruitment

Future development of a direct relationship between age-0 abundance and recruitment seems most likely for the Kodiak region (Fig. 5). In this region, linear relationships were evident for the average, log-transformed, nonzero density and for the overall mean density. There was no convincing evidence of a direct linear relationship between mean length and recruitment.

Table 3

Results from two ANOVA tests used to examine year (1985–88) and region (Kodiak versus Shumagin) effects on age-0 pollock density in the western Gulf of Alaska. The first ANOVA was on log-transformed densities and the second was on rank-transformed densities.

Source	df	MS	F	P
ANOVA, log-transformed fish densities				
year	3	9.072	5.3893	0.0013
region	1	0.805	0.4782	0.4898
year × region	3	9.204	5.4679	0.0011
error	296	1.683		
ANOVA, rank-transformed fish densities				
year	3	70809	6.3609	0.0003
region	1	1374	0.1234	0.7256
year × region	3	66291	5.9550	0.0006
error	296	11132		

Discussion

The geographic distribution of age-0 fish integrates the effects of dispersal of young from spawning areas and of spatial differences in mortality; therefore, it helps reveal

Table 4

Probabilities from Fisher's LSD tests, which followed the ANOVA tests summarized in Table 3. The hypothesis that means of transformed age-0 densities are equal was rejected if $P<0.00313$. This reflects a Bonferroni correction of the 0.05 overall alpha level (e.g. 0.05/16). Significantly different pairs of means are indicated by probabilities in bold.

	Comparison by year						Comparison by region
	Kodiak region			Shumagin region			
	1985	1986	1987	1985	1986	1987	Kodiak vs. Shumagin
P-values, log-transformed fish densities							
1985							0.16537
1986	0.11119			0.05592			0.46505
1987	**0.00079**	0.06104		0.31479	0.45564		**0.00307**
1988	0.00716	**0.00018**	**0.00000**	0.10872	0.97748	0.53177	0.00665
P-values, rank-transformed fish densities							
1985							0.21982
1986	0.03708			0.02599			0.49393
1987	**0.00159**	0.21323		0.41495	0.22086		0.00441
1988	**0.00294**	**0.00001**	**0.00000**	0.11894	0.73141	0.45407	**0.00253**

Table 5

ANCOVA results of region, year and day effects on the mean length per haul of age-0 pollock collected from two regions, Kodiak and Shumagin, in the western Gulf of Alaska during August–October, 1985–88. Length was weighted by fish density.

Source	df	MS	*F*	*P*
Year	3	35036	73.907	0.0000
Region	1	37407	78.907	0.0000
Year × Region	3	1211	2.555	0.0560
Day	1	144833	305.518	0.0000
Error	247	474		

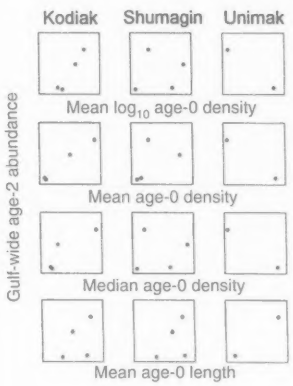

Figure 5

Gulf-wide age-2 pollock abundance (from Table 1) plotted against the regional indices of age-0 abundance and size (from Table 2) for the 1985–88 year classes of pollock in the Gulf of Alaska.

major recruit pathways. In the GOA, the largest aggregation of spawning pollock occurs in Shelikof Strait; and the FOCI recruit-pathway paradigm shows that larvae are carried southwestward from this area (Hinckley et al., 1991; Hermann et al., 1996a, 1996b; Kendall et al., 1996). However, the widespread occurrence of age-0 pollock throughout the areas surveyed, and probably beyond, indicates that the FOCI recruit-pathway paradigm needs to account for more complex dispersal, multiple spawning areas, and possible geographic differences in mortality.

The FOCI recruit-pathway paradigm was expanded to the early juvenile stage by Hinckley et al. (1991) with the inclusion of age-0 distribution data. Their study, however, included only data from 1987. It is now apparent that the age-0 distribution during 1987 was more geographically skewed than in other years during 1985–88. Perhaps this skewed distribution relates to sea surface drift in the greater GOA, which may have been rapid during 1987 (Ingraham et al., 1998), although larval distributions in the Shelikof Strait vicinity seemed normal (Kendall and Picquelle, 1990; Hinckley et al., 1991; Bailey et al., 1996c). Regardless, the 1985 and 1988 age-0 distribution data suggest that the FOCI recruit-pathway paradigm should include the Kodiak Island vicinity as part of the principal nursery for young pollock in the GOA.

Deep countercurrent flows (Reed et al., 1987; Stabeno et al., 1995), eddies (Schumacher and Kendall, 1995), reten-

tion near shore, and possible directed movements by juveniles all complicate "typical" southwestward dispersal of pollock eggs and larvae from Shelikof Strait. For example, the high age-0 densities around Kodiak Island during 1985 may be explained by high larval abundances upstream of the main spawning area (Kendall and Picquelle, 1990), which in turn may reflect northeastward transport of eggs at depth in the countercurrent. On the other hand, the high age-0 densities around Kodiak during 1988 are more difficult to explain. Countercurrent flows have been detected off the Gulf-side of Kodiak Island (Musgrave et al., 1992) but historically this is not an area of high egg or larval abundance. Furthermore, widespread occurrences of high age-0 density suggest that dispersal was both downstream and upstream, or that some fish originated from elsewhere.

The existence of multiple spawning areas further complicates our understanding of pollock recruitment pathways. Sporadic survey effort by the NMFS indicates that spawning occurs at a number of different locations throughout the western GOA between Prince William Sound and Unimak Pass. The percentage of pollock biomass in non-Shelikof spawning areas was 10, 21, 19, 29, and 14% of the total in all areas surveyed in 1989, 1990, 1994–96, respectively (Williamson[5]; Karp[6]; Wilson et al.[7], and references therein). These estimates are conservative because not all known spawning areas were surveyed each year and survey timing may not have coincided with peak spawning. In addition, other surveys of pollock, summarized by Bechtol,[9] indicate that the biomass of prespawning aggregations in Prince William Sound ranged from 28,855 to 114,344 metric tons during 1995, 1997, and 1998. Although these surveys occurred after 1988 and conditions may have changed during the intervening period, it seems likely that at least some age-0 pollock were spawned in areas outside of Shelikof Strait. Estimating relative production, however, is difficult because it is impossible to identify where individual recruits were spawned and because of spatial variations in the processes that remove prerecruits from the GOA. As indicated by studies of other species (Pulliam and Danielson, 1991; Frank, 1992), the relationships among these different spawning groups could be very complex.

The use of age-0 densities in the Kodiak region in forecasting recruitment suggests that "atypical" dispersal of young from Shelikof Strait and production of fish from other spawning areas may be relevant factors in understanding GOA pollock recruitment. Admittedly, this use is based on only a few years of data. However, Smith et al. (1984) reported age-0 densities for the 1980–82 year classes in some bays within the Kodiak region that corresponded with year-class strength estimates. Furthermore, if sampling method is ignored, a time series of mean age-0 density near northeast Kodiak Island is available for the 1980–88 year classes, except 1983, and it corresponds reasonably well with recruitment (Pearson, r=0.74, P=0.04, n=8) (author's unpubl. data). The Shumagin and Unimak regions were comparatively less promising for predicting recruitment, although the relative strength of the 1985 and 1988 year classes was indeed evident among the Shumagin densities. Age-0 fish from both the Kodiak and Shumagin regions may move into Shelikof Strait during winter as indicated by large aggregations of age-1 fish observed there during early spring (McKelvey, 1996). This movement probably involves a relatively constant proportion of the Kodiak and Shumagin age-0 populations because their abundance as age-1 fish in Shelikof Strait continues to be indicative of recruitment (McKelvey, 1996; Guttormsen and Wilson[10]). Farther southwest, in the Unimak region, juveniles may leave the GOA sometime after their first summer. This movement may explain why age-0 densities in the Unimak region during 1987 and 1988 had no relation to recruitment despite a 7-fold variation in subsequent year-class strength.

Given their relevance to recruitment, age-0 pollock around Kodiak Island warrant closer consideration. As previously discussed, some may come from Shelikof Strait. Others may move downstream from spawning areas such as those in or near Prince William Sound and Resurrection Bay (Nelson and Nunnallee, 1985; Muter and Norcross, 1994; Norcross and Frandsen, 1996; Karp[6]). Downstream drift is probable given the distance, currents (Schumacher and Reed, 1980; Stabeno et al., 1995), spawning time (Muter and Norcross, 1994), and estimated age-0 ages.[11] Drift from eastern areas may be relatively important to establishing age-0 populations along the upstream- and Gulf-side of Kodiak Island when the influx of Shelikof fish is low. Retention of young along this part of Kodiak Island may be facilitated by shoreward flows and vortices created by topographical influences on the prevailing current (Lagerlof, 1983; Dunn et al.[4]). Local spawning is another possible source of age-1 pollock as evidenced by adults in prespawning condition in Marmot Bay, which is on northeast Kodiak Island (Karp[6]; Williamson[12]).

The relatively large size of many age-0 fish may reflect favorable conditions in the Kodiak Island vicinity because size is generally regarded as having a positive effect on survival. Walters et al. (1985) first reported a southwest-to-northeast increase in age-0 size; however, a more rigorous

[9] Bechtol, W. R. 1998. Prince William Sound walleye pollock: current assessment and 1999 management recommendations. Regional Information Report No. 2A98-41, 25 p. Alaska Department of Fish and Game, Division of Commercial Fisheries Management and Development, 333 Raspberry Rd., Anchorage, AK 99518.

[10] Guttormsen, M., and C. Wilson. 1998. Echo integration-trawl survey results for walleye pollock in the Gulf of Alaska during 1998. *In* Stock assessment and fishery evaluation report, p. 509–530. Prepared by the Gulf of Alaska Groundfish Plan Team, North Pacific Fishery Management Council, P.O. Box 103136, Anchorage, AK 99510.

[11] Mean age of age-0 pollock in the Kodiak region during 1985–88 ranged from 127 to 143 d. These estimates are based on age-0 length and length-age relationships for the same age-0 populations (Bailey et al., 1996b), to which mortality-adjusted density weights were applied.

[12] Williamson, N. 1999. Personal commun. National Marine Fisheries Service, 7600 Sand Point Way NE, Seattle, WA 98115.

comparison with their study is complicated by differences in gear and survey strategy. One possible explanation for the effect of region on fish size is growth rate variability. Growth rates, estimated from larval and juvenile length-at-age data, were found to increase from southwest to northeast, at least during 1987 (Yoklavich and Bailey, 1990; Brown and Bailey, 1992). Prey quality (Merati and Brodeur, 1996), and physical conditions (Strickland and Sibley, 1989) have also been observed to vary, the supposition being that the Kodiak Island area is a richer nursery habitat than are more southwestern areas. Variation in time of spawning is another possibility; particularly in 1986 and 1988, when regional differences in growth were not evident (Bailey et al., 1996b). It appears, however, that time of spawning throughout the western GOA is fairly synchronous (Picquelle and Megrey, 1993; Muter and Norcross, 1994), except near the Shumagin Islands were it happens about one month earlier (Wilson et al.[7]). Size-related migration and mortality are other possible effects on fish size but evidence is lacking.

Spatial differences in size may translate into spatial differences in mortality. In a review of size-selective mortality among juvenile fishes, Sogard (1997) identified over-winter mortality and predation as major size-selective processes. These mortality vectors may be particularly strong because the first-winter growth of juvenile pollock in the GOA is negligible (Brodeur and Wilson, 1996a), and predation is prevalent (Brodeur and Bailey, 1996). Thus, geographic differences in age-0 size may contribute a spatial component to year-class strength determination. The poor relationship between age-0 size and year-class strength, however, suggests that age-0 size is a minor factor, at least in terms of determining relative recruitment among year classes.

The practice of targeting echo layers was a drawback of these data. This practice has been shown to bias estimates of fish density (Wilson et al., 1996), but its effect on distribution patterns is uncertain. It is possible that the area represented by mean fish density varied with year and region, thereby causing density to be a poor indicator of abundance. Estimates of year- and region-specific density were, however, closely related to the absolute abundance estimates of Bailey and Spring (1992) (Pearson, r=0.78, P=0.008, n=10). On the positive side, the practice of targeting echo sign does reduce the effort needed to collect biological samples (Brodeur and Wilson, 1996b), but this must be carefully weighed against possible adverse effects.

In summary, age-0 pollock appear to have been evenly distributed throughout much of the western GOA during 1985–88, except during 1987 when a strong, east-to-west increase in fish density was observed. The Kodiak region was an important pollock nursery despite its position upstream from what is presumed to be the most important spawning area in the GOA. The Kodiak region was particularly well suited as a recruitment predictor owing, perhaps, to a relative abundance of large-size individuals. Questions emerged about annual variability in the origin and dispersal of young pollock, and regarding the possibility that geographic effects on survival or retention could affect the relative production of GOA recruits among different spawning areas.

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Use of the original von Bertalanffy growth model to describe the growth of barramundi, *Lates calcarifer* (Bloch)

Yongshun Xiao

SARDI Aquatic Sciences Centre
2 Hamra Avenue
West Beach
Southern Australia 5024, Australia
E-mail address: yongshun.xiao@bigpond.com

Abstract—In the original von Bertalanffy growth equation, the rate of change in body mass of an individual is assumed to result from two opposing biological processes: anabolism and catabolism. Because this differential equation cannot be solved analytically, some of its analytically solvable special cases are commonly used, despite their restrictive assumptions. In this study, I used a generalization of the original von Bertalanffy growth equation and some of its commonly used special cases to estimate parameters from a set of tagging data on times at liberty, lengths at release, and lengths at recapture of a centropomid perch (*Lates calcarifer*) and provide a method for determining the anabolic and catabolic rates of animals in their natural environment. Fitting the original von Bertalanffy growth equation to the tagging data suggests that a 1% increase in body mass of the fish corresponds to a 0.8721% increase in anabolic rate and a 1.0357% increase in catabolic rate. Alternatively, *L. calcarifer* may be interpreted as exhibiting a strong seasonality in growth: it grows fastest in length at the start of autumn, grows less until a full stop in the middle of winter, shrinks until the middle of spring, and then resumes a positive growth for another cycle. Consequently, it is unnecessary to use the analytically solvable special cases of the original von Bertalanffy growth equation in data analysis, unless their assumptions are validated. I also explain why Pauly's index of growth performance is adequate and propose an index of catabolic performance.

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Information on the growth of animals is important for studying their population dynamics, physiology, and biochemistry (Peters, 1983; Calder, 1984; Schmidt-Nielsen, 1984; Reiss, 1989; Xiao, 1998). Many empirical models have been developed to describe the growth of animals macroscopically, including the Gompertz (1825) and logistic growth models (Verhulst, 1838). By contrast, von Bertalanffy (1938) proposed a somewhat mechanistic growth model for body mass $W(a) \geq 0$ of an individual of age a, of the form

$$dW(a)/da = AW(a)^B - CW(a)^D,$$

where A, B, C and D = positive biological constants;
$AW(a)^B$ = the rate of anabolism (building up of body mass) at age a; and
$CW(a)^D$ = the rate of catabolism (breaking down of body mass) at age a.

Thus, in this model, the rate of change in body mass of an individual $dW(a)/da$ at age a is assumed to result from two opposing biological processes (anabolism and catabolism). Although the underlying mechanisms may be too complicated for $dW(a)/da$ to be approximated or even interpreted as such, this differential equation has opened up a line of thought for integrating the macroscopic growth of animals with certain physiological and biochemical processes (Pauly, 1981). Also, it is fairly general, includes almost all previous deterministic growth models as its special cases, and forms a basis for identifying the "right" growth models from amongst all its special cases. Consequently, some work has been done to estimate parameters A, B, C, and D to determine the anabolic and catabolic rates of fish (Ursin, 1967; Pauly, 1981).

However, because the differential equation cannot be solved analytically, its analytically solvable special cases are so commonly used that one simple special case has become known in the fisheries literature as *the* von Bertalanffy growth equation (Xiao, 1996). Nonetheless, assumptions for its various analytically solvable special cases can be very restrictive. Indeed, although assumed to take a value of $^2/_3$ in that simple special case (Pauly, 1981), constant B can take any value from $^2/_5$ to $^5/_7$, because B is often assumed to satisfy $\beta(B-1)+1=0$ and because B in Equation 2 below is known to take any value from $2^1/_2$ to $3^1/_2$. It is also possible that catabolic rate is not proportional to body mass (i.e. $D \neq 1$). In any case, it is best not to make any assumptions about the values of A, B, C, and D.

Like most growth models, the von Bertalanffy (1938) growth equation is age-dependent. Although it can be modified to consider, implicitly, the seasonal growth of animals and the effects of tagging, a general framework was not available for explicitly incorporating time and time-dependent factors (i.e. ambient temperature and food availability) in age-dependent growth models. This prompted Xiao (1999) to derive general age- and time-dependent growth models for animals and to give a comprehensive list of their commonly used special cases. Such models explicitly incorporate age, time, and their de-

pendent factors and are useful for modeling growth at age and time (e.g. from length-at-age data), incremental growth at age and time increment (e.g. data on length increment at age and time increment from tagging studies), the effects of tagging, and, if coupled with a proper age- and time-dependent population dynamics model, the effects on the growth of animals of many population characteristics, such as population size.

Because of experimental constraints, such as difficulties in taking continuous measurements (if measured at all), anabolic and catabolic rates of animals are necessarily measured either by restraining them in the laboratory or in the field. Such restraints can cause stress to animals and hence result in biased measurements. Experimental methods should be developed to estimate the anabolic and catabolic rates of animals in as natural an environment as possible.

In this study, I use an age- and time-dependent von Bertalanffy (1938) growth equation and some of its commonly used special cases for estimating the parameters from a set of tagging data on times at liberty, lengths at release, and lengths at recapture of a centropomid perch, barramundi (*Lates calcarifer*) and provide a method for determining the anabolic and catabolic rates of animals in their natural environment. I also explain why Pauly's (1981) index of growth performance is adequate and propose an index of catabolic performance.

Model

Let $0 \le W(a,t) < \infty$, $-\infty < a_0 \le a < \infty$, $-\infty < t_0 \le t < \infty$, denote the body mass of an individual of age a at time t, with an arbitrary reference age a_0 and an arbitrary reference time t_0. The von Bertalanffy (1938) growth equation can be generalized as

$$\frac{dW(a,t)}{dt} = A(a,t)W(a,t)^B - C(a,t)W(a,t)^D, \quad (1)$$

where $A(a,t) \ge 0$ and $C(a,t) \ge 0$ = functions of age a and time t; and
B and D = positive biological constants.

For a particular functional form of $A(a,t)$ and $C(a,t)$, Equation 1 can be used for estimating its parameters from data on body masses of animals of different ages at different times, or on two distinct body masses of the same individual at different times. If collected at all, such data are collected mostly for terrestrial and occasionally for aquatic animals. What is most commonly gathered for both terrestrial and aquatic animals is, however, one or more linear dimensions of an individual's body, such as its total length at age, or two distinct measurements at different times. Measurements of linear dimensions of an animal contain useful information on its body mass. Indeed, it is well known that body mass $W(a,t)$ is scaled allometrically to body length $L(a,t)$, i.e.

$$W(a,t) = \alpha L(a,t)^\beta, \quad (2)$$

where α and β = (constant) allometric parameters (Peters, 1983; Calder, 1984; Schmidt-Nielsen, 1984; Reiss, 1989).

Substitution of Equation 2 into Equation 1 yields

$$\frac{dL(a,t)}{dt} = \frac{1}{\beta}\alpha^{B-1}A(a,t)L(a,t)^{\beta(B-1)+1} - \frac{1}{\beta}\alpha^{D-1}C(a,t)L(a,t)^{\beta(D-1)+1}. \quad (3)$$

Thus, if α and β are known, as is usually assumed, parameters B and D, and those in $A(a,t)$ and $C(a,t)$ can be estimated from data on length-at-age data, or on two distinct lengths of the same individual at different times.

Although too general to be solved even numerically, Equations 1 and 3 are useful in formulating ideas. Now, I consider a special case of Equations 1 and 3 for seasonally varying $A(a,t)$ and $C(a,t)$, such that

$$A(a,t) = \frac{\gamma}{K}\left[K + b\cos\left(\frac{2\pi}{T}(t - t_\phi)\right)\right] \text{ and}$$

$$C(a,t) = K + b\cos\left(\frac{2\pi}{T}(t - t_\phi)\right),$$

where γ, $\gamma b/K$, T, and t_ϕ are, respectively, the mean, amplitude, period, and time shift for the anabolic process; K, b, T, and t_ϕ are, respectively, the mean, amplitude, period, and time shift for the catabolic process. For this special case, Equations 1 and 3 then become, respectively

$$\frac{dW(a,t)}{dt} = \left[K + b\cos\left(\frac{2\pi}{T}(t - t_\phi)\right)\right] \times \left[\frac{\gamma}{K}W(a,t)^B - W(a,t)^D\right] \quad (4)$$

and

$$\frac{dL(a,t)}{dt} = \frac{1}{\beta}\left[K + b\cos\left(\frac{2\pi}{T}(t - t_\phi)\right)\right] \times \left[\frac{\gamma}{K}\alpha^{B-1}L(a,t)^{\beta(B-1)+1} - \alpha^{D-1}L(a,t)^{\beta(D-1)+1}\right]. \quad (5)$$

Equations 4 and 5 can be solved numerically but not analytically. For comparison and illustration, I now consider five special cases (four of which are reparameterizations of commonly used growth equations) of Equation 5:

If $b=0$, or if $A(a,t)$ and $C(a,t)$ are constants, Equation 5 becomes

$$\frac{dL(a,t)}{dt} = \frac{1}{\beta}\left(\gamma\alpha^{B-1}L(a,t)^{\beta(B-1)+1} - K\alpha^{D-1}L(a,t)^{\beta(D-1)+1}\right). \quad (6)$$

If $\beta(B-1)+1=0$ (i.e. $B-1=-1/\beta$) and $\beta(D-1)+1=1$ (i.e. $D=1$), Equation 5 becomes

$$\frac{dL(a,t)}{dt}=\frac{1}{\beta}\left[K+b\cos\left(\frac{2\pi}{T}(t-t_s)\right)\right]\left(\frac{\gamma}{K}\alpha^{-1/\beta}-L(a,t)\right), \quad (7)$$

the solution of which as an initial value problem, with $L(a,t)|_{t=t_0}=L(t_0+a-t,t_0)$ for $a-a_0\geq t-t_0$ or with $L(a,t)|_{a=a_0}=L(a_0,a_0+t-a)$ for $a-a_0<t-t_0$, yields

$$L(a,t)=\begin{cases}\frac{\gamma}{K}\alpha^{-1/\beta}-\left(\frac{\gamma}{K}\alpha^{-1/\beta}-L(a_0,t-a+a_0)\right) & \\ \times\exp\left(-\frac{K}{\beta}(a-a_0)-\frac{bT}{\beta\pi}\sin\left(\frac{\pi}{T}(a-a_0)\right)\right. & a-a_0<t-t_0\\ \left.\times\cos\left(\frac{2\pi}{T}\left(t-t_s-\frac{1}{2}(a-a_0)\right)\right)\right) & \\ \frac{\gamma}{K}\alpha^{-1/\beta}-\left(\frac{\gamma}{K}\alpha^{-1/\beta}-L(t_0+a-t,t_0)\right)\exp\left(-\frac{K}{\beta}(t-t_0)\right. & a-a_0\geq t-t_0\\ \left.-\frac{bT}{\beta\pi}\sin\left(\frac{\pi}{T}(t-t_0)\right)\cos\left(\frac{2\pi}{T}\left(t-t_s-\frac{1}{2}(t-t_0)\right)\right)\right). & \end{cases} \quad (8)$$

Similar age-dependent models have been given, *inter alia*, by Appeldoorn (1987), Pauly et al. (1992), Fontoura and Agostinho (1996), and Xiao (1999). Also, notice that bT (in Appeldoorn (1987) and Pauly et al. (1992), $b=C$ and $T=1$) is a dimensionless quantity and is useful for interspecific comparison of the strength of seasonal growth oscillations (Pauly, 1984, 1985, 1990).

If $\beta(B-1)+1=0$ (i.e., $B-1=-1/\beta$), $\beta(D-1)+1=1$ (i.e., $D=1$), and $b=0$, Equation 5 becomes

$$L(a,t)=\begin{cases}\frac{\gamma}{K}\alpha^{-1/\beta}-\left(\frac{\gamma}{K}\alpha^{-1/\beta}-L(a_0,t-a+a_0)\right) & \\ \times\exp\left(-\frac{K}{\beta}(a-a_0)\right) & a-a_0<t-t_0\\ \frac{\gamma}{K}\alpha^{-1/\beta}-\left(\frac{\gamma}{K}\alpha^{-1/\beta}-L(t_0+a-t,t_0)\right) & \\ \times\exp\left(-\frac{K}{\beta}(t-t_0)\right), & a-a_0\geq t-t_0\end{cases} \quad (9)$$

a reparameterization of what is commonly called in the fisheries literature the von Bertalanffy (1938) growth equation.

If $\beta(B-1)+1=0$ (i.e., $B=1$) and $\beta(D-1)+1=2$ (i.e. $D-1=1/\beta$), Equation 5 becomes

$$\frac{dL(a,t)}{dt}=\frac{\gamma}{\beta K}\left[K+b\cos\left(\frac{2\pi}{T}(t-t_s)\right)\right]\times L(a,t)\left(1-\frac{L(a,t)}{\frac{\gamma}{K}\alpha^{-1/\beta}}\right), \quad (10)$$

the solution of which as an initial value problem, with $L(a,t)|_{t=t_0}=L(t_0+a-t,t_0)$ for $a-a_0\geq t-t_0$ or with $L(a,t)|_{a=a_0}=L(a_0,a_0+t-a)$ for $a-a_0<t-t_0$, yields

$$L(a,t)=\begin{cases}\left[\frac{1}{\frac{\gamma}{K}\alpha^{-1/\beta}}-\left(\frac{1}{\frac{\gamma}{K}\alpha^{-1/\beta}}-\frac{1}{L(a_0,t-a+a_0)}\right)\right.\\ \times\exp\left(\frac{\gamma}{\beta}(a-a_0)-\frac{\gamma bT}{\beta K\pi}\sin\left(\frac{\pi}{T}(a-a_0)\right)\right.\\ \left.\left.\times\cos\left(\frac{2\pi}{T}\left(t-t_s-\frac{1}{2}(a-a_0)\right)\right)\right)\right]^{-1} & a-a_0<t-t_0\\ \left[\frac{1}{\frac{\gamma}{K}\alpha^{-1/\beta}}-\left(\frac{1}{\frac{\gamma}{K}\alpha^{-1/\beta}}-\frac{1}{L(t_0+a-t,t_0)}\right)\right.\\ \times\exp\left(-\frac{\gamma}{\beta}(t-t_0)-\frac{\gamma bT}{\beta K\pi}\sin\left(\frac{\pi}{T}(t-t_0)\right)\right.\\ \left.\left.\times\cos\left(\frac{2\pi}{T}\left(t-t_s-\frac{1}{2}(t-t_0)\right)\right)\right)\right]^{-1}, & a-a_0\geq t-t_0\end{cases} \quad (11)$$

a reparameterization of the seasonal logistic growth equation (Xiao, 1999).

If $\beta(B-1)+1=1$ (i.e., $B=1$), $\beta(D-1)+1=2$ (i.e., $D-1=1/\beta$), and $b=0$, Equation 5 becomes

$$L(a,t)=\begin{cases}\left[\frac{1}{\frac{\gamma}{K}\alpha^{-1/\beta}}-\left(\frac{1}{\frac{\gamma}{K}\alpha^{-1/\beta}}-\frac{1}{L(a_0,t-a+a_0)}\right)\right.\\ \left.\times\exp\left(-\frac{\gamma}{\beta}(a-a_0)\right)\right]^{-1} & a-a_0<t-t_0\\ \left[\frac{1}{\frac{\gamma}{K}\alpha^{-1/\beta}}-\left(\frac{1}{\frac{\gamma}{K}\alpha^{-1/\beta}}-\frac{1}{L(t_0+a-t,t_0)}\right)\right.\\ \left.\times\exp\left(-\frac{\gamma}{\beta}(t-t_0)\right)\right]^{-1}, & a-a_0\geq t-t_0\end{cases} \quad (12)$$

a reparameterization of the logistic growth equation (Xiao, 1999).

Data and analysis

Equations 8, 9, 11, and 12 are segmented functions (Xiao, 1999); they provide flexibility in analysis of growth data. Thus, by appropriately choosing the value of time t (which is a relative quantity), one can use either segment ($a-a_0<t-t_0$ or $a-a_0\geq t-t_0$) for an individual animal or for a group of individuals, or use both segments ($a-a_0<t-t_0$ and

$a - a_0 \geq t - t_0$) for a group of individuals. It is, however, more convenient to use only one segment in a single analysis. Indeed, although growth parameters can be estimated by use of either segment of any of Equations 8, 9, 11, and 12, it is easier to use the segment for $a - a_0 < t - t_0$, by letting time t start before the animals whose growth is to be modeled are born, unless time is allowed to take negative values. Use of the other segment, i.e. that for $a - a_0 \geq t - t_0$, gives identical results, but it requires first calculating $L(t_0 + a - t, t_0)$.

The amount of data required to estimate parameters in a growth model is a function of the generality of that model: the more general a model is, the more data it usually requires. Age- and time-dependent growth models generally require knowledge of two ages a_0 and a, time t, and two sizes $L(a_0, t - a + a_0)$ and $L(a,t)$ if $a - a_0 < t - t_0$; or knowledge of two times t_0 and t, age a, and two sizes $L(t_0 + a - t, t_0)$ and $L(a,t)$ if $a - a_0 \geq t - t_0$. However, use of Equations 4, 5, 8, and 11 only requires knowledge of the difference between two ages $a - a_0$, time t, and two sizes $L(a_0, t - a + a_0)$ and $L(a,t)$; or of the difference between two times $t - t_0$, time t, and two sizes $L(t_0 + a - t, t_0)$ and $L(a,t)$. By contrast, use of Equations 9 and 12 only requires knowledge of the difference between two ages, $a - a_0$, and two sizes, $L(a_0, t - a + a_0)$ and $L(a,t)$, or of the difference between two times $t - t_0$, and two sizes $L(t_0 + a - t, t_0)$ and $L(a,t)$.

Interestingly, a reparameterization of Equation 9 has been widely used to model tagging data (Xiao, 1999), where a_0 or t_0 is interpreted as time at release, a or t as time at recapture, $a - a_0$ or $t - t_0$ as time at liberty, $L(a_0, t - a + a_0)$ or $L(t_0 + a - t, t_0)$ as size at release, and $L(a,t)$ as size at recapture. It has also been used extensively to model size-at-age data (obtained, say, by aging animals by reading marks in scales and otoliths) (e.g. Moulton et al., 1992), where a_0 or t_0 is interpreted as age at birth, a or t as age, $L(a_0, t - a + a_0)$ or $L(t_0 + a - t, t_0)$ as size at birth, and $L(a,t)$ as size at age. However, it is rare to know two ages and the corresponding sizes of an animal; what are commonly measured are one age and its corresponding size. Consequently, it is common practice to fit Equation 9 to such size-at-age data to estimate age at birth a_0 or t_0, as well as the growth parameters, thereby implicitly assuming, for all animals concerned, that the size at birth $L(a_0, t - a + a_0)$ or $L(t_0 + a - t, t_0)$ is zero and that the age at birth a_0 or t_0 is the same. Exactly the same argument applies to Equation 12.

The barramundi *L. calcarifer* is a protandrous fish found in estuaries and other coastal areas of the Indo-West Pacific (Griffin, 1987). Between August 1977 and June 1980, 4933 barramundi with a body total length range of about 10–100 cm were captured by a combination of lure fishing, tidal trap, seine and gill net. Fish were measured to the nearest cm, tagged with Floy FT-2 dart tags for fish >35 cm and FD-67 anchor tags for fish <35 cm, and released in rivers flowing into the Van Diemen Gulf and the Gulf of Carpentaria of northern Australia (Davis and Reid, 1982). Of those tagged, 312 of a total length of 23–92 cm with a mean of 60 ±13 (mean ±SE) cm were recaptured, but only 308 were used in the analysis below due to incomplete recapture information. The time at liberty ranged from zero to 932 d, with a mean of 219 ±211 d, and the length increment from –21 to 35 cm, with a mean of 6 ±8 cm. Negative increments in length are often observed in a tagging experiment, because tagged animals can shrink in size immediately after tagging, or because of recording errors at both release and recapture. The estimates of allometric parameters for barramundi, used in the present paper, were those obtained by Reynolds (1978): $\hat{\alpha}=1.06 \times 10^{-5}$ kg $\times$cm$^{-\hat{\beta}}$ and $\hat{\beta} = 3.02$.

Let a_0 or t_0 denote time at release, a or t time at recapture, $a - a_0$ or $t - t_0$ time at liberty, $L(a_0, t - a + a_0)$ or $L(t_0 + a - t, t_0)$ the length of a fish at release, and $L(a,t)$ its length at recapture. Equation 6 and the segments of Equations 8, 9, 11, and 12 for $a - a_0 < t - t_0$, were fitted to the tagging data, by using the nonlinear least squares method, under the assumptions that T=365.25 d, time started (i.e. time t=0) on 1 January 1960 (see Xiao [1999] for its significance), and errors in $L(a,t)$ follow independent normal distributions, with a mean of $\dot{L}(a,t)$ and a constant variance of σ^2 (Table 1). In these calculations, Equation 6 was numerically solved as an initial value problem with $L(a, t)|_{t = t_0} = L(t_0 + a - t, t_0)$ for $a - a_0 \geq t - t_0$ using the fourth order Runge-Kutta method (Beyer, 1978). A likelihood ratio test suggests that Equation 8 is significantly different from Equation 9 ($F_{2,304}$=48.6892, P<0.0001); and Equation 11 is significantly different from Equation 12 ($F_{2,304}$=45.3460, P<0.0001). Thus, Equations 8 and 11, and their associated estimates of parameters seem adequate for describing the tagging data. Selection among Equations 6, 8, and 11 is difficult because little is known of the underlying mechanisms of the growth process.

Discussion

Fitting of the original von Bertalanffy growth model (Eq. 6) to the tagging data for barramundi suggests that its anabolic rate changes proportionally with the $\hat{B}$=0.8721 power of its body mass and that its catabolic rate changes proportionally ($\hat{D}$=1.03567≈1) with its body mass (i.e. at a 1:1 ratio). Such an estimate of B is 9.0125% higher than that ($\hat{B}$≈4/5) obtained for many fish under laboratory conditions (Pauly, 1981). More data are needed to examine the generality of this finding. By contrast, little information is available on the value of D. Nonetheless, it is interesting that the catabolic rate of barramundi increases proportionally with its body mass; a 1% increase in body mass corresponds to about a 1% increase in catabolic rate. Consequently, it is unnecessary to use the analytically solvable special cases of the original von Bertalanffy growth equation in data analysis, unless their assumptions are validated.

Alternatively, like many tropical and subtropical species of fish (Appeldoorn, 1987; Pauly et al., 1992), barramundi may be interpreted as exhibiting a strong seasonal growth. For both models (Eqs. 8 and 11), its growth rate reaches its maximum on 3 or 4 March (i.e. at the start of autumn), slows down to zero on 17 July (i.e. in the middle of winter), reaches its minimum on 2 or 3 September (i.e. at the start of spring), returns to zero on 19 or 20 October (i.e. in the middle of spring), and comes back to its maxi-

mum rate on 3 or 4 March (i.e. at the start of autumn) (Fig. 1). Thus, its length grows fastest on 3 or 4 March (i.e. at the start of autumn), grows less until a full stop on 17 July (i.e. in the middle of winter), shrinks until 19 or 20 October (i.e. in the middle of spring), and resumes a positive growth for another cycle. Thus, barramundi does not grow in length for three months in a year, from 17 July (i.e. in the middle of winter) to 19 or 20 October (i.e. in the middle of spring). However, Equations 8 and 11 have different assumptions and predict different amplitudes of seasonally varying growth rate. Such a strong seasonality in growth rate might be related to seasonal changes in the availability of food and in water temperature.

Similarly, tagging may adversely affect the growth of barramundi perch and bias estimates of parameters in a growth model, where its effects are not taken into proper account. In fact, Xiao (1994) has already interpreted the same set of data in terms of the effects of tagging. However, it is impossible to identify the right model from all possible models, because of the inductive nature of modeling and because of our poor understanding of the underlying mechanisms of growth and how tagging affects growth. In a preliminary analysis, I have constructed a model, and have attempted (but failed) to estimate, simultaneously, both the effects of tagging and seasonally varying growth rates. Such a failure is not surprising because the amount of information in a set of tagging data is limited. Further progress can be made only by better understanding the underlying mechanisms of growth.

This work also puts some of Pauly's (1981) work into perspective. For example, $\alpha^{-1/\beta}\gamma/K$ and K/β in Equation 9 can be interpreted respectively as the average maximum size and growth rate of a species. As Pauly (1981) proposed, the product $(\alpha^{-1/\beta}\gamma/K)(K/\beta) = \alpha^{-1/\beta}\gamma/\beta$ is indeed an index of growth performance because it is in direct proportion to the mean anabolic rate. Similarly, $\alpha^{-1/\beta}\gamma/K$ and γ/β in Equation 12 can be interpreted respectively as the average maximum size and growth rate of a species. The quotient $(\gamma/\beta)/(\alpha^{-1/\beta}\gamma/K) = \alpha^{1/\beta}K/\beta$ is an index of catabolic performance, because it is in direct proportion to the mean catabolic rate.

Finally, anabolic and catabolic rates of animals can be estimated from data from a mark-recapture experiment on two distinct lengths of the same individual measured at different times. Thus, the present work has demonstrated a way to estimate anabolic and catabolic rates of animals. Such field-based estimates can be compared with those obtained under laboratory conditions.

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Table 1

Estimates and (in parentheses) standard errors of parameters obtained by fitting Equations 6, 8, 9, 11, and 12 to barramundi tagging data using the least squares method under the assumptions that T=365.25 d, time started (i.e. time t=0) in 1 January 1960, and errors in $L(a,t)$ follow independent normal distributions, with a mean of $\hat{L}(a,t)$ and a constant variance of σ^2. P<0.0001; n=308.

Equation	$\hat{\gamma}$ (kg^{1-D}/d)	$\hat{K}$ (kg^{1-D}/d)	$\hat{b}$ (kg^{1-D}/d)	$\hat{t}_0$ (d)	$\hat{B}$	$\hat{D}$	df_1, df_2, F	$\hat{\sigma}^2$	r^2
6	0.00843 (0.00008)	0.00556 (0.00005)	—	—	0.87213 (0.00148)	1.03567 (0.00216)	4,304,15424.6096	22.9793	0.9951
8	0.00474 (0.00052)	0.00184 (0.00034)	0.00265 (0.00054)	62.7197 (6.8279)	—	—	4,304,20333.2966	17.4525	0.9963
9	0.00500 (0.00062)	0.00196 (0.00040)	—	—	—	—	2,306,30966.0441	22.8923	0.9951
11	0.00446 (0.00036)	0.00206 (0.00023)	0.00302 (0.00045)	63.5155 (6.7581)	—	—	4,304,19947.9059	17.7884	0.9962
12	0.00487 (0.00044)	0.00228 (0.00028)	—	—	—	—	2,306,30895.5175	22.9443	0.9951

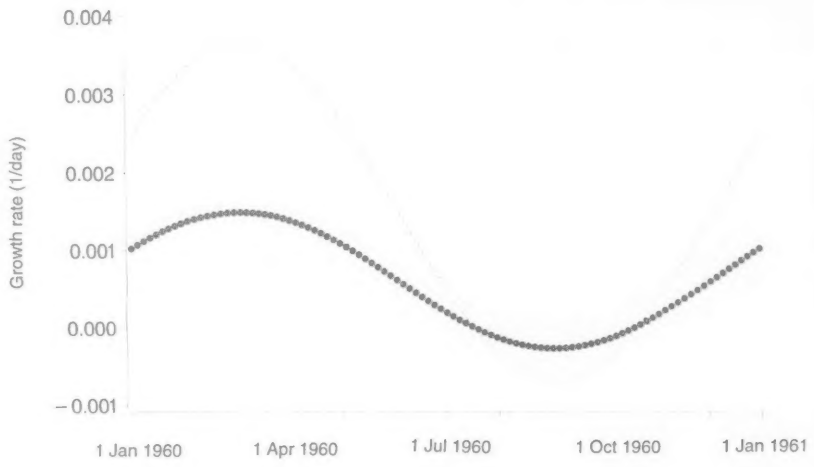

Figure 1

Growth rate $\frac{1}{\beta}\left[K + b\cos\left(\frac{2\pi}{T}(t - t_s)\right)\right]$ in Equation 8 (•••••) and growth rate $\frac{\gamma}{\beta K}\left[K + b\cos\left(\frac{2\pi}{T}(t - t_s)\right)\right]$ in Equation 11 (-----), both as a function of time t, with estimates of parameters γ, K, b, and t_s in Table 1 for barramundi, and T=365.25 d.

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The relation between spawning area and biomass of Japanese pilchard, *Sardinops melanostictus*, along the Pacific coast of Japan

Hiromu Zenitani

National Research Institute of Fisheries and Environment of Inland Sea
2-17-5, Maruishi, Ohno-cho Saeki-gun,
Hiroshima, 739-0452 Japan
E-mail address: zenitani@nnf.affrc.go.jp

Sakutaro Yamada

Tokyo University of Fisheries
4-5-7, Konan, Minato-ku,
Tokyo, 108-0075 Japan

Abstract–When stocks are depleted, direct assessments of population levels are not only difficult but may be highly inaccurate. The work reported here was motivated by the need to manage the collapse of the far eastern sardine (*Sardinops melanostictus*) population. Spawning area was chosen as the first indicator of population size because the spatial spread of the stock increases when the spawning population increases. Our objective was to clarify the relation between spawning area and the spawning biomass of this species off the Pacific coast of Japan in order to estimate biomass with the spawning area data.

The pilchard spawning area (A_I) in a given year was calculated by summing the areas of 1° longitude × 1° latitude squares where early developmental stage eggs were present. The optimal relationship between A_I and the spawning biomass (B) was $A_I=2.518 B^{0.4610}$, not a simple linear relationship. One cause of the nonlinear relationship seemed to be that pilchard egg aggregations were distributed over space in a patchy manner.

Finally, we introduced an approximate method for estimating the pilchard spawning biomass by using the inverted equation of the optimal relationship between A_I and B; ($B=0.135A_I^{2.1691}$).

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Japanese pilchard, *Sardinops melanostictus* (known as "Japanese pilchard" in Japan) is found off the Pacific coast of Japan and is an important commercial species. The pilchard stock has fluctuated widely over a period of several decades (Kondo et al., 1976). The annual catch in Japan peaked at 1.5 × 10^6 metric tons (t) in the 1930s, but decreased to only 3.0 × 10^4 t in the 1960s. It recovered to 4.6 × 10^6 t in the 1970s and reached the second highest peak for this century in 1988. However, the catch in 1995 fell to one-tenth of that in 1988 (Fig. 1).

When stocks are depleted, direct assessments of population levels are not only difficult but may be highly inaccurate (Hewitt et al.[1]). In such situations, an alternative method of population assessment is to survey egg or larval populations as a means of estimating biomass (e.g. the egg production method; Lasker, 1981). However, the egg production method (EPM) is expensive and time consuming (Mangel and Smith, 1990).

A biological characteristic of the Japanese pilchard is that its distribution range changes in accordance with stock size. During pilchard stock size increases, the distributional range expands widely (Wada and Kashiwai, 1991). In contrast, when stock size is declining, the distributional range may became quite limited (Hiramoto, 1981). The spawning grounds of Japanese pilchard are known to expand with egg abundance increases and contract with abundance declines (Watanabe et al., 1996; Zenitani et al., 1998). In general, as the spawning population increases, the spatial spread of the stock also increases (Rosenzweig, 1981; MacCall, 1988). Therefore, the area of spawning grounds (spawning area) was chosen as the first indicator of pilchard population recovery (Smith, 1973; Smith and Hewitt, 1985).

Our objective was to clarify the relationship between pilchard spawning area and spawning biomass off the Pacific coast of Japan, to estimate biomass with spawning area data. Moreover, to explain why the relationship between pilchard spawning area and spawning biomass formed, we used a model in which a patchy egg distribution was assumed.

Materials and methods

Spawning area and spawning biomass

Intensive egg surveys of coastal pelagic fish have been conducted every year since 1978 by the Fisheries Agency of Japan (Mori et al., 1988; Kikuchi and Konishi, 1990; Ishida and Kikuchi, 1992;

[1] Hewitt, R., A. Bindmann, and N. C. Lo. 1984. Procedures for calculating the egg production estimate of spawning biomass. Administrative Report LJ-84-19, Southwest Fisheries Center, La Jolla, CA 92038-0271.

Zenitani et al., 1995). Among these surveys, two governmental institutions, the National Research Institute of Fisheries Science and the Nansei National Fisheries Research Institute, have collaborated on surveys covering the inshore and offshore waters between 128–143°E and 28–36°N since 1978 (Fig. 2). We used data from these surveys covering the waters along the Pacific coast of Japan between 130–142°E and 28–36°N (Fig. 3). In the census, from 149 to 344 ichthyoplankton samples were collected each year by towing two types of conical or cylindrical-conical nets (inside mouth diameter: 45 or 60 cm; mesh aperture: 0.335 mm). Each net was retrieved vertically at 1 m/s from 150 m depth or from the bottom at stations shallower than 150 m.

We calculated two kinds of pilchard spawning area (A_1 and A_2). Pilchard spawning is concentrated into two months, February and March (Watanabe et al., 1996). Therefore, A_1 in any given year was calculated by summing the areas of 1° longitude × 1° latitude squares where early developmental *A*-stage eggs, as categorized by Nakai (1962), were collected during February and March. A_2 was calculated by summing the areas of 1° longitude × 1° latitude squares where eggs of any stage were collected during February and March. The length of time elapsing from fertilization to the end of the *A* stage at the different temperatures, 15.2°, 17.5°, and 20.3°C, are 25, 16, and 10 hours, respectively. The length of time elapsing from fertilization to hatching at the different temperatures, 15.2°, 17.5°, and 20.3°C, are 85, 56, and 34 hours, respectively (Nakai, 1962).

We used the pilchard biomass estimated along the Pacific coast of Japan from 1977 to 1995 by Wada and Jacobson (1998). Biomass estimation was conducted by virtual population analysis (VPA) with the catch-at-age data of the purse-seine fishery. The biomass estimate was for the middle of June, the end of the major spawning season for Japanese pilchard. During the main spawning season, most spawning is done by age-1+ pilchards and a small amount is done by age-1 pilchards (Hiramoto, 1981). The biomass of age-1+ pilchards in year $y-1$ was assumed to be the spawning biomass (B) in year y.

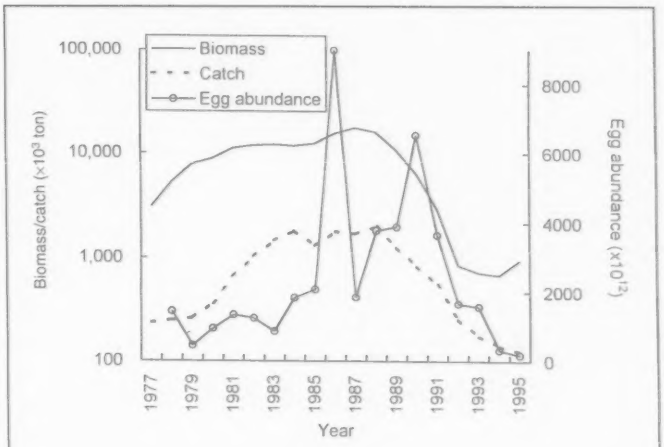

Figure 1

Catch, spawning biomass, and egg abundance of Japanese pilchard along the Pacific coast of Japan from 1978 to 1995 (after Wada and Jacobson, 1998).

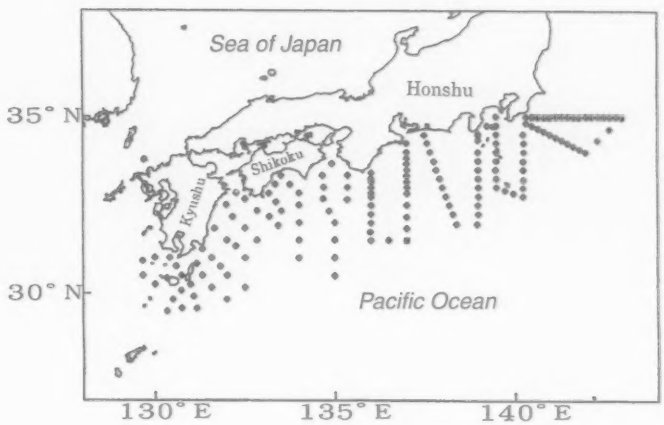

Figure 2

An example of station allocation for the spawning survey of Japanese pilchard in February and March 1994.

Model

To test whether spawning area could be correlated with spawning biomass, statistical analyses were performed. We used five relationships between A (=A_1 or A_2) and B: $A=f(B)$

I $f(B)=u_1B$,
II $f(B)=u_1B+u_2$,
III $f(B)=u_1B^{u2}$,
IV $f(B)=u_1\,exp(u_2B)$, and
V $f(B)=A_s[1-\{u_1/(u_1+u_2B)\}^{u1}]$,

where u_1, u_2 and A_s were parameters.

Relationship V was obtained by a modification of Mangel and Smith's (1990) model. They used the negative binomial model to describe the contagion of pilchard eggs. It is commonly used in ecological modeling (Pielou, 1977; Zweifel and Smith, 1981; Mangel and Smith, 1990; Zenitani et al., 1998). Mangel and Smith (1990) extended the negative binomial model to include the possibility of failure to detect eggs which are present at a station. According to Mangel and Smith (1990),

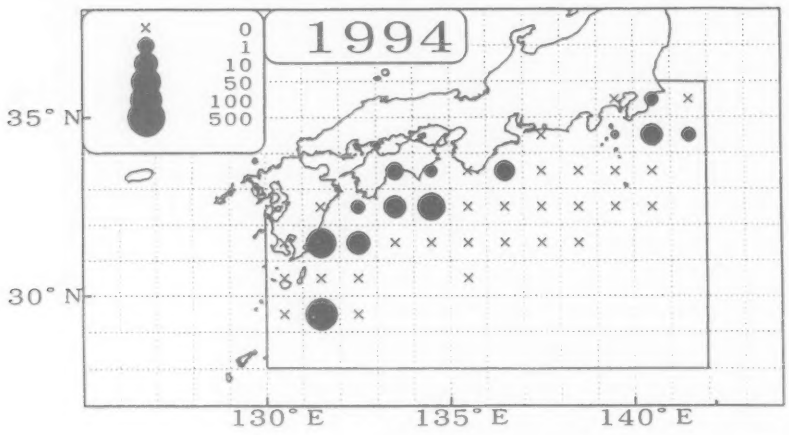

Figure 3

Distribution of pilchard eggs along the Pacific coast of Japan in February and March 1994. Solid circles and crosses show the mean egg density (number of eggs per 0.159 m^2) in 1° × 1° squares. Data in the area surrounded by the bold lines was used for the analysis (after Zenitani et al., 1998)

$$E\{N_p\} = N\alpha p\left[1-\{k/(k+m\omega)\}^k\right], \quad (1)$$

where N_p and N = number of samples with a positive number of eggs and total number of samples in survey area (A_s), respectively;

α and ω = sampling efficiency parameters;

p = probability that a observation station is a habitat for spawning stock;

k = the over-dispersion parameter of negative binomial distribution; and

m = mean number of eggs at a habitat area for spawning stock.

To simplify, we assumed that $\alpha = 1$, $p = 1$, and $\omega = 1$. Moreover, we assumed that the spawning biomass (B) and total egg abundance (m N) is linearly related, that is $B = \delta m N$, where δ is a constant. Actually, a linear relationship exists between the spawning biomass and egg abundance of the Japanese pilchard (Fig. 4). We assumed that a survey area (A_s) is equally divided by N stations. Because N_p is a random variable, the observed spawning area $A=A(N_p)=\gamma N_p$ is also a random variable, where γ is a proportional constant ($=A_s/N$).

From Equation 1, we thus obtain

$$E\{A\} = \gamma E\{N_p\}$$
$$= A_s\left[1-\{k/(k+\varepsilon B)\}^k\right],$$

where $\varepsilon = 1/(N\delta)$

If $u_1 = k$, $u_2 = \varepsilon$, $A_s = 640$ (10^3 km^2), and $A - E\{A\}$, we have relationship V between A and B.

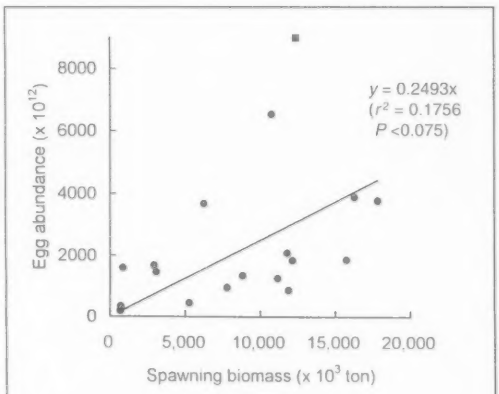

Figure 4

Relationship between the egg abundance and spawning biomass of Japanese pilchard (after Wada and Jacobson, 1998).

Parameters estimation, confidence interval analysis, and selection of the optimal relationship

We assumed that each relationship (I–V) had an error term z; $\ln(A)=\ln(f(B))+\ln(z)$; that z had a log-normal distribution; $\ln(z) \sim N(0,\sigma^2)$; and that $N(0,\sigma^2)$ has a normal distribution of mean zero and variance σ^2. z will take only positive values, so we expected the mean of z, $E\{z\}=\exp(\sigma^2/2)$, to be larger than 0. In addition, the log-normal distribution has a long tail, which is common with ecological data (Hilborn and Mangel, 1997).

Table 1

Estimated parameter values and 95 % confidence intervals (in parentheses) for each relationship between the spawning area (A_I: 10^3 km^2) and the spawning biomass (B: 10^3metric ton) of Japanese Pilchard along the Pacific Coast of Japan from 1978 to 1995.

Relationship		u_1	u_2	A_s (10^3/km^2)	AIC
I	$A_I=u_1B$	0.02318 (0.023109–0.023240)			41.2
II	$A_I=u_1B+u_2$	0.01204 (0.012012–0.012059)	50.048 (49.9144–50.1824)		11.2
III	$A_I=u_1B^{u2}$	2.518 (2.5157–2.5208)	0.4610 (0.46087–0.46110)		4.2*
IV	$A_I=u_1 exp(u_2B)$	69.604 (69.5169–69.7246)	0.00007941 (0.00079270–0.000079560)		18.0
V	$A_1 = A_s\left[1-\left\{u_1/(u_1+u_2B)\right\}^{u_2}\right]$,	0.1283 (0.12801–0.128509)	0.0001516 (0.00015124–0.00015194)	640	4.3

Asterisk (*) indicates that the relationship is optimal.

Parameter estimation and confidence interval analysis were performed by the following procedure. u_1 and u_2 were estimated by minimizing the sum of squares:

$$\Theta = \sum_y \left(\ln(A_y / \hat{A}_y)\right)^2,$$

where A_y and $\hat{A}_y$ = the observed spawning area in year y and predicted values from relationships I– V, respectively.

The least-squares minimization was performed by the quasi-Newton method in Solver, which is "add in" software for MS-Excel (Microsoft Corp., 1996). The least-squares minimization procedure was stopped if either of the two following conditions were satisfied:

more than 100 iterations were attempted; or

the sum of squared residuals changed by less than 0.01% between iterations.

Confidence intervals of the estimators were calculated through a likelihood ratio test. If $\ln(A_y/\hat{A}_y) \sim N(0,\sigma^2)$, then

$U = (u_1, u_2)$ is a parameter vector,
$\hat{U} = (\hat{u}_1, \hat{u}_2)$ is the estimated parameter vector which minimizes the Θ, and
$\hat{U}_I = (u_i, \hat{u}_2)$ is the parameter vector which minimizes the Θ with respect to a certain value of u.

The confidence interval for a certain parameter u_i was given as the region which satisfied the inequality $2\ln[L(\hat{U})/L(U)] \leq x^2(0.95,1)$, where L and $\chi^2(0.95,1)$ were the likelihood and 95% value of the χ^2 distribution with one degree of freedom, respectively. The Akaike information criterion (AIC) was used for selecting an optimal relationship within the set of proposed relationships I–V. The AIC is calculated for candidate models, and the most parsimonious one has the lowest AIC (Akaike, 1973).

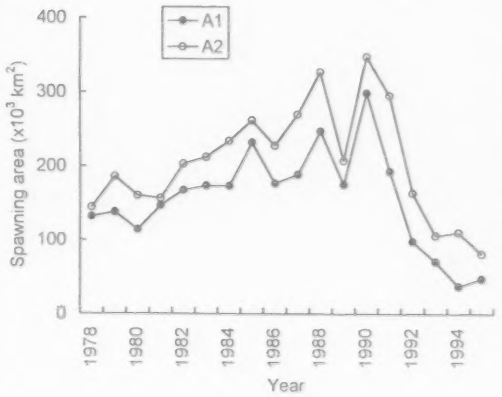

Figure 5

Change in the spawning area of the Japanese pilchard along the Pacific coast of Japan over time. A_1 and A_2 were calculated by summing the areas of 1° longitude × 1° latitude squares where early developmental stage eggs and eggs of any stage occurred, respectively.

Results

The spawning biomass (B) of the Japanese pilchard experienced a remarkable increase in the 1970s, peaked in 1988, and has been declining since the end of the 1980s (Fig. 1; Wada and Jacobson, 1998). A_I expanded from 114,000 km^2 in 1980 to 299,000 km^2 in 1990 , before shrinking to 38,000 km^2 in 1994 (Fig. 5). Estimated parameters, their confidence intervals for each relationship, and AIC are summarized in Table 1. The value of AIC was at a minimum in relationship III and varied considerably compared to the

Table 2

Estimated parameter values and 95% confidence intervals (in parentheses) for each relationship between the spawning area (A_2: 10^3 km^2) and the spawning biomass (B :10^3metric ton) of Japanese pilchard along the Pacific Coast of Japan from 1978 to 1995.

Relationship		u_1	u_2	A_s (10^3/km^2)	AIC
I	$A_2=u_1B$	0.03196 (0.031853–0.032075)			48.7
II	$A_2=u_1B+u_2$	0.01141 (0.011389–0.011438)	102.382 (102.2073–102.5608)		4.7
III	$A_2=u_1B^{u2}$	12.304 (12.2926–12.3154)	0.3156 (0.31546–0.31567)		0.9*
IV	$A_2=u_1 exp(u_2B)$	116.780 (116.5000–116.9103)	0.00005689 (0.00056782–0.000057001)		7.5
V	$A_2 = A_s\left[1-\left\{u_1/(u_1+u_2B)\right\}^{u_1}\right]$,	0.1176 (0.11737–0.117766)	0.0004710 (0.00046983–0.00047289)	640	3.3

other relationships, except for V. The optimal relationship between A_1 and B was A_1=2.518 $B^{0.4610}$ (Table 1, Fig. 6), although the difference in AIC between relationship III and V was small. Relationship III was statistically significant (r^2=0.833, n=18, P<0.001). A_2 expanded steadily from 144,000 km^2 in 1978 to 327,000 km^2 in 1988 (Fig. 5). The area decreased to 208,000 km^2 in 1989, peaked at 349,000 km^2 in 1990, and then shrank to 82,000 km^2 in 1995. The optimal relationship between A_2 and B was A_2=12.304 $B^{0.3156}$ (Table 2, Fig. 6) and was statistically significant (r^2=0.737, n=18, P<0.001).

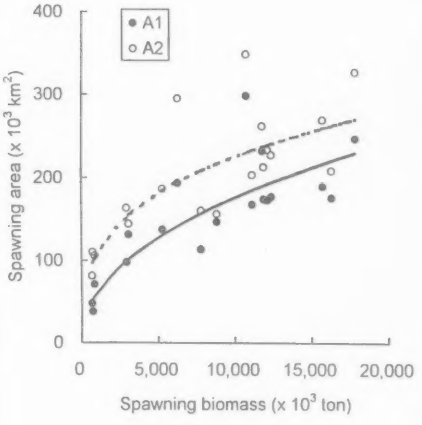

Figure 6

Relationship between the spawning area (A_1 or A_2) and spawning biomass of Japanese pilchard. Closed circles = the spawning area (A_1), open circles = the spawning area (A_2). The solid line indicates the optimal relationship between A_1 and the spawning biomass (B) (A_1=0.2518$B^{0.4610}$). The dotted line indicates the optimal relationship between A_2 and the spawning biomass (A_2=12.304$B^{0.3156}$).

Discussion

The spatial distribution of pilchard eggs may increase over time through transportation by wind-driven currents or the Kuroshio frontal eddy current (Kasai et al., 1992). Because the data for calculating A_2 included the presence of eggs at stages long after spawning had occurred, A_2 was an overestimate of the spawning area. Therefore, A_1 may be a better indicator of the spawning area than A_2. The relationship between A_1 and A_2 was A_1 = 0.8501 A_2 –18.468, and was statistically significant (r^2=0.900, n=18, P<0.001). However, the calculation of A_1 was more expensive and time consuming because egg developmental stages need to be distinguished. Selection of the indicator will depend on our demand for the precision of biomass estimate.

One cause of the nonlinear relationship between the spawning area and spawning biomass seemed to be that pilchard egg aggregations are distributed over space in a patchy manner, in relation of course to the schooling behavior of the adults. Judging from the small difference in AIC between relationship III and V (Table 1) and the similar shapes of III and V (Fig.7), we believed that the model which assumes a patchy egg distribution seemed reasonable.

An estimate of pilchard spawning biomass can be obtained by using the inverted relationship of III (B= $0.135A_1^{2.1691}$). This estimate of spawning biomass might be useful as an abundance index for tuning VPA, such as the adaptive framework described by Gavaris (1988). Frequently, fisheries managers must estimate the biomass of pelagic stocks. Several techniques of abundance estimation may be successfully applied to the pilchard, including the egg production method, acoustic surveys, systematic aerial surveys, or combinations of these (Watanabe, 1983; Hara, 1983; Hara, 1986). Selection or devel-

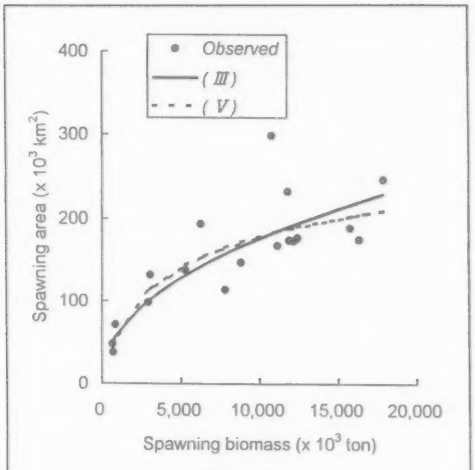

Figure 7

Difference between relationships III and V. Closed circles indicate the observed data. The solid line indicates relationship III (A_1=0.8029$B^{1.8077}$, AIC=4.2). The dotted line indicates relationship V (A_1=640[1 − {0.1283/(0.1283/0.1283 + 0.0001516 B)}$^{0.1283}$], AIC=4.3).

opment of methods will depend on management goals, performance of the resource in recovery, and fishery development. We believe that the method in our study provides a new tool for the estimation of Japanese pilchard biomass when information concerning the fishery is limited.

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Geographic patterns in growth of the giant Pacific sea scallop, *Patinopecten caurinus*

Steve Ignell
Evan Haynes
Auke Bay Laboratory
Alaska Fisheries Science Center
National Marine Fisheries Service, NOAA
11305 Glacier Highway
Juneau, Alaska 99801-8626
E-mail address: Steve.Ignell@noaa.gov

Giant Pacific or weathervane sea scallops, *Patinopecten caurinus*, were first fished commercially in the Gulf of Alaska in 1967, when 3449 kg of unshucked sea scallops (estimated 341 kg of meats) were landed at Kodiak, Alaska (Haynes and Powell, 1968). The discovery of commercially exploitable stocks of giant Pacific sea scallops led to a fishery that expanded rapidly, and landings increased to 856 metric tons (t) of schucked meats by 1969 (ADF&G, 1979). For the next two decades, scallop landings fluctuated greatly (ADF&G, 1987), a result of limited stocks, restrictive regulations, and more lucrative opportunities in other Alaska fisheries (Kaiser, 1986). Since 1990, however, the fishery has changed from a part-time fleet to a dedicated full-time fleet with the influx of larger, more efficient vessels. This change has led to sustained near-record harvests (up to 823 t) and the adoption of new management measures for the fishery (Shirley and Kruse, 1995; NMFS[1]).

Most of the biological literature on giant Pacific scallops relates to fishing exploration (Rathjen and Rivers, 1964; Haynes and Powell, 1968; Ronholt and Hitz, 1968; Haynes and McMullen, 1970; Bourne, 1988), aquaculture (Beattie, 1985; Thompson et al., 1985; Rhee, 1989), or reproductive biology (Hennick, 1970 and 1971; Robinson and Breese, 1984). Age and growth of giant Pacific scallops have been studied in populations off Oregon (Starr and McCrae, 1983), Washington and the Strait of Georgia (Haynes and Hitz, 1971), northern Gulf of Alaska (Kaiser, 1986; Hennick[2]), and the lower Cook Inlet region (Hammarstrom and Merritt, 1985).

A lack of data on biological productivity has affected recent efforts to develop a fishery management plan (FMP) for Alaska giant Pacific scallop stocks (NMFS[1]). It has inhibited the development of yield models and a numeric specification of overfishing (an FMP requirement) and resulted in a simple numeric range given for optimal yield. However, there is a renewed interest in acquiring better information for stock assessments and biological parameters needed to implement an exploitation-rate harvest strategy for the fishery (NMFS[1]).

This note presents results of a comparative growth study of stocks of giant Pacific scallops in the Gulf of Alaska. Samples for this study were collected during the initial explorations for commercial quantities of these scallops in 1968 (Haynes and Powell, 1968); thus these data yield prefishery biological parameters that can provide a baseline to evaluate fishery impacts on the giant Pacific scallop populations in Alaska.

Methods

Giant Pacific scallops were collected at six locations in the Gulf of Alaska from 27 April to 6 June 1968 (Fig. 1). Sampling was done from the chartered FV *Viking Queen* with a standard New Bedford type sea scallop dredge 3.96 m wide (equipped with 10-cm rings). A detailed description of this type of gear is given in Posgay (1957) and Bourne (1964). The locations and depths of sampling were 1) on Albatross Bank at 92–104 m, 2) on Marmot Flats at 73–104 m, 3) in lower Cook Inlet at 108–122 m, 4) off Cape St. Elias at 91–102 m, 5) off Ocean Cape at 82–91 m, and 6) off Lituya Bay at 64–75 m. Areas were selected for their geographic separation and likely abundance of scallops. Giant Pacific scallops were shucked aboard the vessel, and the upper valves were retained for age and growth analyses. At each location, 59–248 scallops were selected (Table 1); the only criterion for selection was that each sample include a wide range of sizes. Because larger (and rarer) scallops were more likely to be chosen, samples were not selected at random. Within a sample, however, the range of sizes at any given age was not great; for the purpose of fitting growth curves, we assumed that each age class was sampled randomly.

Ages were determined by counting clearly visible annuli (growth rings) on the outer surface of the upper valve. The first annulus is formed halfway during the second year of life; scallops spawn in the summer and the annuli are formed in the winter (Haynes and Hitz, 1971). This aging method has been used extensively to study mollusk growth, such as in studies on the North Atlantic sea scallop, *Placopecten magellanicus* (Stevenson, 1934; Stevenson and Dickie, 1954; Merrell et al., 1961), and on the European sea

[1] National Marine Fisheries Service. 1996. Fishery management plan for the scallop fishery off Alaska. Unpubl. document. Natl. Mar. Fish. Serv., P.O. Box 21668, Juneau, AK 99802, 123 p.

[2] Hennick, D. P. 1973. Sea scallop, *Patinopecten caurinus*, investigations in Alaska. Commer. Fish. Res. Develop. Act, project 5-23-R, completion rep. (unpubl.). Alaska Dep. Fish and Game, Juneau, AK 99801, 38 p.

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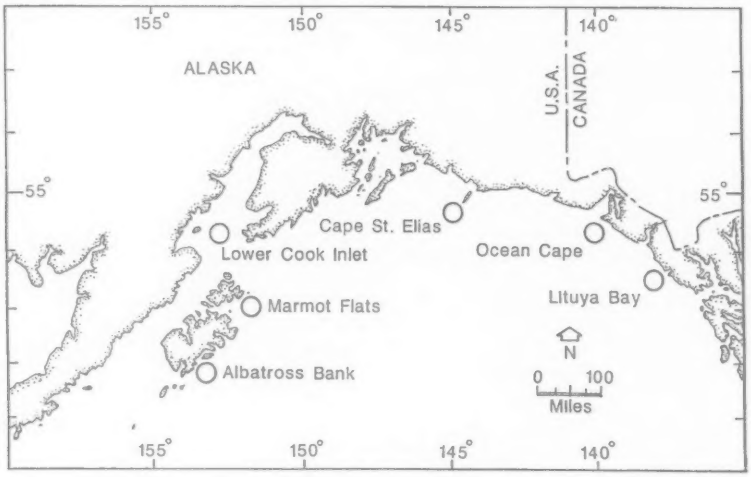

Figure 1

The six areas in the Gulf of Alaska sampled for giant Pacific sea scallops during the *Viking Queen* survey, 1968.

scallop, *Pecten maximus* (Gibson, 1956; Mason, 1957), and shows reasonably good agreement with "true" (isotopically predicted) ages when growth rings are clearly visible (Dare and Deith, 1989). Application of the method to *Patinopecten caurinus* has been verified by Haynes and Hitz (1971).

Terminal shell heights (size of shell to the last annulus; hereafter called "shell heights") were used to fit a growth model for each sample (Table 1). No attempt was made to determine the sex of the scallops because of indications that growth differences between sexes were insignificant.[3] After our sampling, scientists of the ADF&G provided sex and age data for scallops taken in August 1970 northwest of Kodiak Island. The von Bertalanffy growth model was fitted to these data, and growth differences between sexes were tested as described in the following section.

Estimation and fitting of von Bertalanffy curves

Mean shell heights by age were plotted for sea scallops in each sample (Fig. 2). Growth decreased steadily with age, suggesting that sigmoid growth was not present or that the shell heights used were beyond the point of inflection; thus the von Bertalanffy growth model was considered appropriate for our study. In this model, length of the i^{th} individual at age t is

$$l_{it} = l_\infty\left[1-e^{-K(t-t_0)}\right]+e_i;\ e_i \sim N(0,\sigma^2).$$

Kimura (1980) showed that maximum likelihood estimation for the von Bertalanffy curve is equivalent to finding least-square estimates of model parameters (see also Cerrato, 1990). Least-square estimates for the three parameters were obtained by nonlinear regression methods. Analysis of residuals showed that the von Bertalanffy model provided an adequate fit for all samples. The precision (variance) of parameter estimates varied with age composition of the sample. For example, samples with few young scallops showed relatively large variances for the parameters K and t_0, whereas samples with few old scallops resulted in imprecise estimates of asymptotic length (Table 2). However, the residual mean square error (MSE), denoting variability about fitted growth equations, did not vary widely among samples.

Comparison of growth curves for different areas

No significant difference (P>0.15) in growth between sexes was detected in the ADF&G samples, supporting the presurvey decision not to determine the sex of the scallops. Growth of scallops from the six areas was compared by likelihood ratio tests by using two probability models: model 1 specified equality of the von Bertalanffy parameters of each area; model 2 allowed separate parameters for each area (Kimura, 1980). The first model consisted of pooling the data over all areas, yielding one growth equation; the second model allowed separate growth equations for each area. Because there was no *a priori* hypothesis concerning growth differences between the areas, 15 simultaneous tests were performed to evaluate pairwise differences in growth. These tests were equivalent to testing k independent hypotheses at a significance level of α. Applying Bonferonni's inequality (Miller, 1966) to the 15 tests resulted in an experimental-wise significance level $\leq k \times \alpha$. We chose α to equal 0.003, giving an experimental-wise significance level of 0.045. Likelihood ratio tests

[3] ADF&G. 1970. Unpubl. observations. Alaska Dept. Fish and Game, Kodiak, AK 99615.

indicated highly significant differences ($P<0.003$) in growth between scallops from each area.

Results and discussion

Sea scallops from the Gulf of Alaska showed a consistent trend in growth geographically: from southeastern Alaska northward and then westward around the perimeter of the Gulf of Alaska, sea scallops tended to be larger. Differences in mean shell height were small at early ages but became more pronounced as the scallops grew older (Fig. 2).

This geographic trend in growth was probably not related to time and depth of sampling. Time of sampling varied little between areas; all areas were sampled within a period of 45 days. Depth of sampling did vary between areas, however, because scallop growth rates are known to vary by water depth, e.g. scallops off Oregon are smaller in deeper waters and have reduced asymptotic lengths (Ronholt and Hitz, 1968; Starr and McCrae, 1983). If this depth-size relationship holds true in Alaska waters, then current estimates of asymptotic size for scallops from the northern areas are biased downwards compared with those from Lituya Bay, where scallops were sampled in shallower waters.

Comparisons of our growth results with two analyses of giant Pacific scallop samples taken after the start of commercial fishing (Kaiser, 1986; Hennick[2]) showed significantly different estimates of asymptotic size. For scallops off Kodiak, values of l_∞ from Hennich's data (182.8 mm) and Kaiser's data (189.8 mm) are larger than our estimate (175.7 mm); for scallops off Yakutat, values of l_∞ from Hennick's data (151.5) and Kaiser's data (143.7 mm) are smaller than our estimate (158.6 mm). Scallop fishing before 1980 occurred entirely in these two areas (Shirley and Kruse, 1995). The reduction in asymptotic size for scallops off Yakutat may indicate an increase in fishing mortality on larger individuals. Both analyses also showed that giant Pacific scallops for a given annular ring are larger from the Kodiak area than from Yakutat, a result that supports our conclusions of geographic growth trends for the giant Pacific sea scallop.

Table 1

Mean shell heights (mm) and standard deviations (SD, in parentheses) and number of giant Pacific sea scallops of given ages sampled from six areas in the Gulf of Alaska. Areas listed are from northwest to southeast.

	Sampling areas											
	Albatross Bank		Marmot Flats		Lower Cook Inlet		Cape St. Elias		Ocean Cape		Lituya Bay	
Age (yr)	Length (SD)	*n*	Length (SD)	*n*	Length (SD)	*n*	Length (SD)	*n*	Length (SD)	*n*	Length (SD)	*n*
1		0		0		0		0		0		0
2		0		0		0		0	51.9 (6.5)	7	37.5 (9.2)	2
3		0		0	70.7 (5.3)	11	77.1 (6.3)	36	76.9 (5.0)	22	69.5 (0.7)	2
4	90.9 (5.8)	47	107.8 (3.3)	4	89.5 (5.5)	19	100.8 (6.4)	21	95.6 (5.7)	117	86.8 (8.3)	62
5	114.2 (4.3)	44	121.2 (3.0)	9	113.1 (6.6)	48	116.6 (6.0)	42	107.1 (5.0)	29	96.9 (7.2)	14
6	134.3 (6.8)	3	137.6 (4.1)	13	127.6 (5.4)	77	135.3 (8.1)	7	117.5 (7.2)	27	110.5 (5.4)	16
7	141.0 (4.5)	21	143.25 (4.8)	8	136.6 (6.0)	58	141.3 (5.2)	4	127.6 (4.5)	11	114.8 (5.6)	33
8	148.8 (3.0)	9	151.6 (2.3)	10	141.3 (6.3)	18	141.0	1	134.5 (7.3)	20	199.7 (6.5)	64
9	157.7 (3.1)	3	156.9 (3.9)	10		0	151.7 (4.5)	3	141.2 (5.9)	9	124.1 (4.2)	9
10	166.0	1	162.5 (0.7)	2		0	152.0	1	144.0 (4.9)	4	129.0 (5.6)	2
11		0	173.0	1		0	153.0	1	155.0	1		0
12		0	166.0 (1.4)	2		0		0		0		0
13		0		0		0	153.0 (0.0)	2		0		0
14		0		0		0	158.5 (4.9)	2		0		0
15		0		0		0	157.0	1		0		0
16		0		0		0		0	156.0	1		0

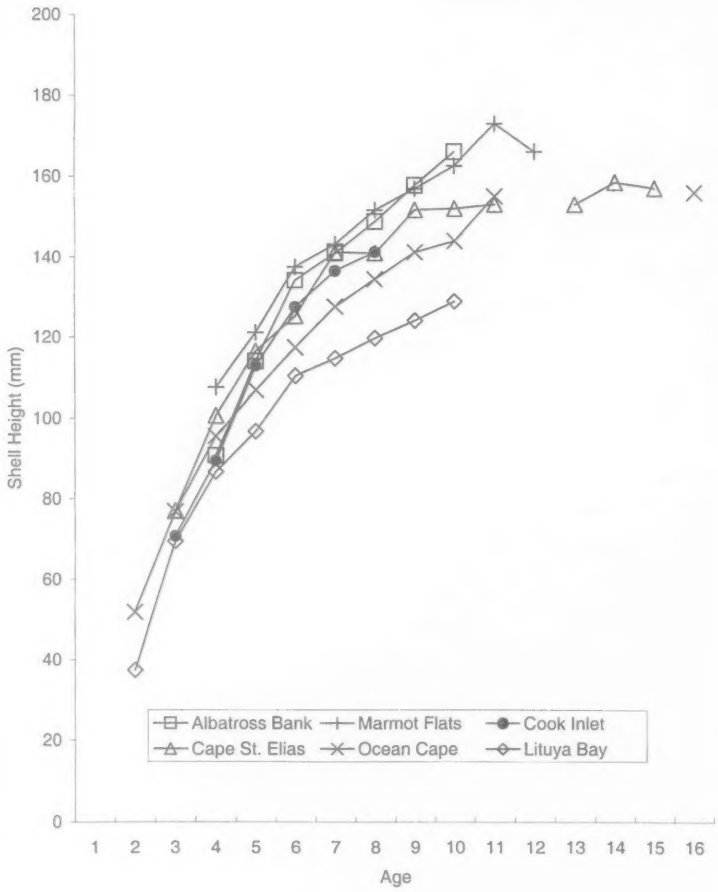

Figure 2

Mean shell heights by age for sea scallops collected in the Gulf of Alaska, 1968.

Table 2

Von Bertalanffy growth parameters (and standard errors) for sea scallops from six Gulf of Alaska areas. Sample areas are given in order from northwest to southeast.

		Parameter estimates (standard errors)			
Area	Sample size	σ^2	L_∞	k	t_0
Albatross Bank	128	23.71	170.1 (4.5)	0.346 (0.035)	1.791 (0.156)
Marmot Flats	59	15.13	175.7 (4.2)	0.265 (0.033)	0.455 (0.387)
Lower Cook Inlet	231	36.88	161.7 (4.1)	0.328 (0.030)	1.353 (0.139)
Cape St. Elias	121	37.64	159.7 (2.8)	0.326 (0.021)	0.974 (0.116)
Ocean Cape	248	34.80	158.6 (3.3)	0.244 (0.017)	0.265 (0.141)
Lituya Bay	204	47.41	130.5 (2.5)	0.367 (0.036)	0.962 (0.207)

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Preliminary examination of the match-mismatch hypothesis and recruitment variability of yellowtail flounder, *Limanda ferruginea*

Donna L. Johnson

James J. Howard Marine Sciences Laboratory at Sandy Hook
Northeast Fisheries Science Center
National Marine Fisheries Service, NOAA
74 Magruder Road
Highlands, New Jersey 07732
E-mail address: Donna.Johnson@noaa.gov

Underlying explanations of recruitment variation among fish stocks have been an issue for several decades. An understanding of biological relationships between larval fish and their zooplankton prey is needed for interpreting recruitment success. Recruitment fluctuations often depend upon events occurring during a critical period between spawning and the time of first feeding by larvae (Hjort, 1914). Conditions affecting these early life stages will also determine the number of individuals that survive in a year class. The timing of spawning can enhance the spatial and temporal affinity between larvae and their food resources (Hjort, 1914; Cushing, 1975, 1990; Cushing and Dickson, 1976).

Once resorption of the yolk sac is complete by yolksac larvae, their survival depends entirely upon the amount and accessibility of available food. If sufficient prey is not located after the yolk sac has become exhausted, permanent degeneration of the larva's digestive system will occur (Pitcher and Hart, 1983). Not only are early stage larvae and young juveniles vulnerable because of their dependence on nourishment, they are also susceptible to movement caused by ocean currents (Hjort, 1914, 1926), predation, and starvation (Houde, 1987).

Yellowtail flounder (*Limanda ferruginea*) is an economically important species that experiences marked variation in year-class strength. In the present study, time series data of fish eggs, larvae, and zooplankton were used to determine if a match or mismatch in time and space between yellowtail flounder production and its potential prey existed from Georges Bank and Southern New England 1977 through 1987. Cushing (1975; 1990) hypothesized that links (matches or misses) in time and space among phytoplankton blooms followed by zooplankton and then larval fish lead to year-class variability. A match occurs when there is a close overlap between production curves of fish larvae and their planktonic prey; conversely, a mismatch occurs when there is an extensive temporal difference (Fig. 1) (Cushing, 1975; 1990). A match of peak occurrences would presumably result in a successful year class owing to adequate feeding and growth, and increased chances for survival if other sources of mortality and loss are constrained.

Yellowtail flounder became a key constituent of the U. S. demersal fishery in the early 1930s as a result of stock declines in winter flounder (Royce et al., 1959). There were subsequent drastic reductions in populations and catches during the early 1970s in Southern New England (SNE) and the mid-1970s in Georges Bank (GB). In SNE stocks, landings declined from 3.5 metric tons (t) in 1970 to 1.5 t in 1975. The abundance of New England groundfish declined by 65% from 1977 to 1987 (NEFC, 1991). Three stocks—haddock, redfish, and yellowtail flounder—reached record low levels by the late 1970s.

The present study is the first attempt to examine interannual variability in yellowtail recruitment in the context of the match-mismatch hypothesis. The goal of this study was to test the prediction of the match-mismatch hypothesis for yellowtail flounder stocks that exist and spawn on Georges Bank (GB) and off Southern New England (SNE) and to observe any correlation between year-class strength and prey abundance. Data from a comprehensive sampling program, the Marine Resources Monitoring, Assessment, and Prediction (MARMAP), structured with broad temporal and geographic coverage, were used for this study. Collections were made during 1977–87 on the U.S. continental shelf from Cape Hatteras to the Gulf of Maine.

Materials and methods

A total of 2496 stations from the western North Atlantic were sampled during an eleven-year period from 1977 to 1987. At each station fish eggs, larvae, and zooplankton were collected with a bongo frame (diameter at the mouth of net: 61 cm) (Posgay and Marak, 1980) fitted with 0.333-mm and 0.505-mm mesh nets and a 45 kg depressor. The volume of water filtered by each net was measured by flowmeters suspended in the center of the net mouth. The plankton nets were lowered at a rate of 50 meters per minute, to within 5 meters of the bottom or to a maximum depth of 200 meters, and retrieved at a rate of 20 meters per minute; nets were towed at 1.5 knots at a 45-degree angle. Net contents were preserved in a mixture of 5% formalin and ocean water. Larvae were measured to within 0.1-mm length increments. For complete descriptions of MARMAP sampling procedures see Sibunka and Silverman (1984, 1989).

For each station, catch values were standardized to the number of individuals under 10 m^2 surface area. The delta distribution (Aitchison, 1955) provided unbiased estimates of sample means (Berrien et al., 1981; Pennington, 1983). The abundance and distribution patterns of yellowtail flounder eggs and larvae were monitored and compared with those of *Calanus* and *Pseudocalanus* prey species in the GB and SNE regions from 1977 to 1987.

Although feeding habit studies of yellowtail larvae have not been docu-

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mented, *Calanus* sp. and *Pseudocalanus* sp. are both dominant representatives of the zooplankton community of the North Atlantic and are important prey for many spring spawned fish larvae (Cushing, 1982; Runge, 1988). The widespread abundance and distribution of *Calanus* and *Pseudocalanus* favor them to be the most likely prey choice of yellowtail flounder larvae. Collectively, monthly distributions and mean densities of zooplankton for May and June coincide with peak occurrences of yellowtail flounder (Figs. 2 and 3). The Spearman's rank-order correlation analysis was used to measure the association between ichthyoplankton and their zooplankton prey.

An adaptation of the "larval food supply model" (Mertz and Myers, 1994) was used to test the match-mismatch hypothesis, the relationship between spawning variability, and the variability of recruitment. The recruitment estimates were obtained from the Northeast Fisheries Science Center (NEFC, 1991). Two aspects were explored: 1) whether or not a relationship exists between spawning duration and recruitment variability and 2) whether deviations from peak spawning between yellowtail flounder larvae and prey are related to recruitment variability.

The mean and standard deviation of observed abundance versus time was calculated for both yellowtail larvae and their prey for each year and for both subareas. The width and overlap of the abundance curves for predator and prey were analyzed. Selected methods from the Mertz and Myers (1994) study were applied for partial use of this analysis. The following parameters—

t_0 = timing between peaks of larval production and food supply;
Δt_0 = annual differences in (t_0) from its mean value;
δ = one-half width of the production period for larvae; and
σ = one-half width of the production period for zooplankton

—were used to calculate 1) variability in peak timing from the mean for individual species (σ and δ), 2) variability in timing between larval spawning and peak zooplankton production (t_0), and 3) year-to-year variability in peak spawning and production (Δt_0). When t_0 = 0, the match between the peak larvae and production of zooplankton is exact (Mertz and Myers, 1994).

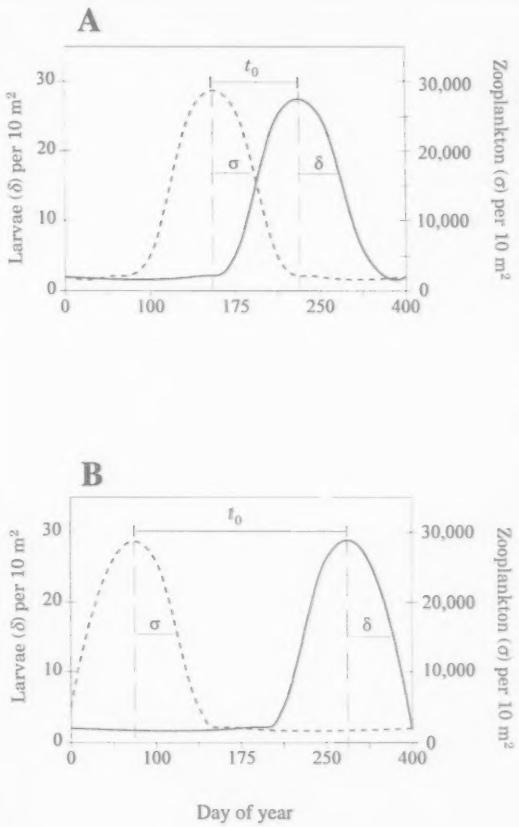

Figure 1

(**A**). A match represented by the overlap of fish larvae and its prey, of the match-mismatch hypothesis. (**B**). A mismatch represented by the lag in time and space between fish larvae and its prey. (δ and σ represent one-half width of the production period of the match-mismatch hypothesis for larvae and zooplankton.) Diagram adapted from Cushing (1990).

Results and conclusions

Variability in timing for individual species

Zooplankton The duration of the *Calanus* sp. peak production (σ) varied from 3.4 to 26.5 days for both subareas. The narrowest distribution occurred during 1984 with 3.4 days, and extremes occurred in 1977 with greater than 12 days for GB and 26.5 days for SNE. The greatest span in peak production for *Pseudocalanus* sp. was 33 days. Smallest duration ranged between 7.8 days (GB) to slightly under 1 day (SNE). The greatest span of time when zooplankton was abundant was 24 days for GB during 1981 and 35 days for SNE during 1982. The low or high zooplankton occurrence was not associated with the strengths or weaknesses of yellowtail recruitment. Both strong (1981) and weak (1982) year classes of yellowtail flounder occurred during times of high variability in peak production of zooplankton.

Ichthyoplankton The difference in timing of peak spawning (Δt_0) from its mean value for yellowtail larvae for both subareas ranged from 1.4 days to approximately 10 days. The largest values of Δt_0 occurred in GB, and again large differences in the timing of spawning did not always reflect years with poor recruitment. Two strong year classes occurred with extreme values of Δt_0: 1977

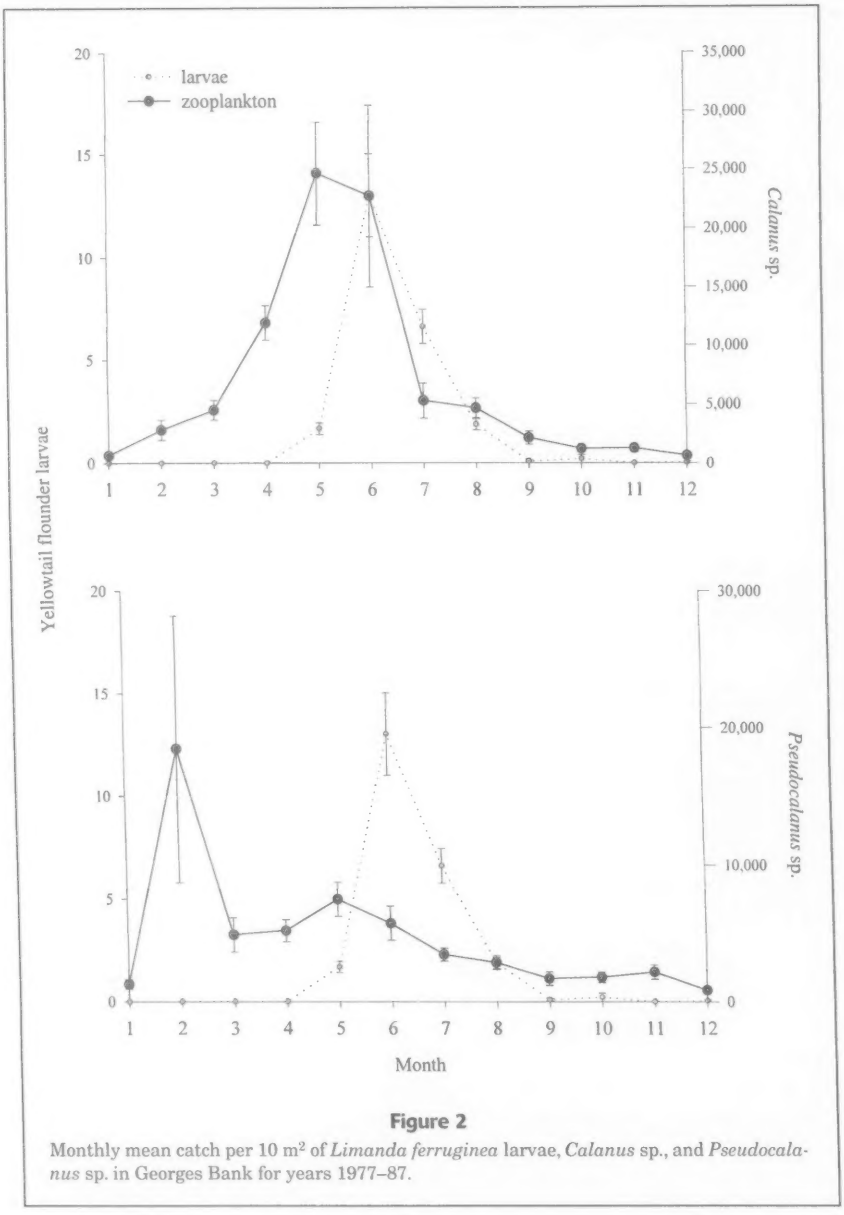

Figure 2

Monthly mean catch per 10 m^2 of *Limanda ferruginea* larvae, *Calanus* sp., and *Pseudocalanus* sp. in Georges Bank for years 1977–87.

with 7 days and 1980 with 3.9 days in GB. In SNE, the weakest year class (1982) possessed the greatest (Δt_0) span with 9.9 days.

Variability in timing between peaks in predator and prey abundance

Examinations of matches and mismatches of larval food and time of yellowtail spawning are shown by the occurrence of width displacements and overlaps from larvae (δ) and its zooplankton prey (σ). The relationship between yellowtail larvae and *Calanus* sp. for SNE display definite matches for years 1980, 1986, and 1987. A slightly larger gap existed between peaks for the year class 1982 (Fig. 4).

During the strong year classes 1980 and 1987, density of yellowtail larvae peaked after that of *Calanus* sp., whereas the reverse occurred in the weaker year classes 1986 and 1982. Similar patterns occurred with the peak spawning and peak production relationships between yellowtail larvae and *Pseudocalanus* sp. The year classes 1982 and

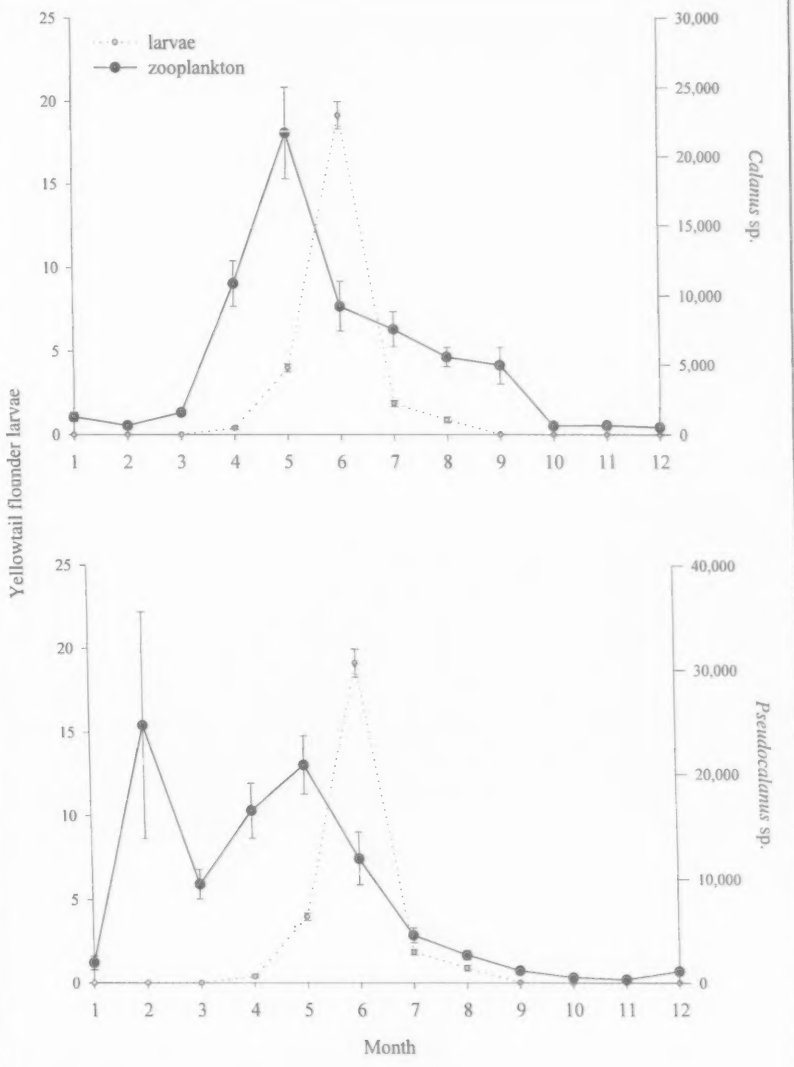

Figure 3

Monthly mean catch per 10 m^2 of *Limanda ferruginea* larvae, *Calanus* sp., and *Pseudocalanus* sp. in Southern New England for years 1977–87.

1987 showed matches in peak spawning and prey production (Fig. 4).

Larger gaps exist between predator and prey in GB for many of the year classes (Fig. 5). There was a temporal gap of almost 56 days between yellowtail flounder and *Calanus* sp. abundance during 1980 and 1982. A slightly smaller mismatch occurred during 1977 at 45 days. The poor year class 1986 had the smallest span in time between predator and prey (16 days) when larvae peaked prior to *Calanus* sp.. For the same year class, 1986, the difference between peaks was slightly greater between larvae and *Pseudocalanus* sp.. There was a smaller mismatch between *Pseudocalanus* sp. and larvae for year class 1982, amounting to 52.6 days (Fig. 5). The stronger year classes, 1977 and 1980, showed more definite matches in spatial timing (<45 days).

To test for a relationship between predator-prey overlap and year-class strength, differences between predator and prey peaks versus year-class strength were plotted for the eleven-year time period (Fig. 6). Two predator and prey combinations (t_0), yellowtail larvae and *Calanus* sp., and

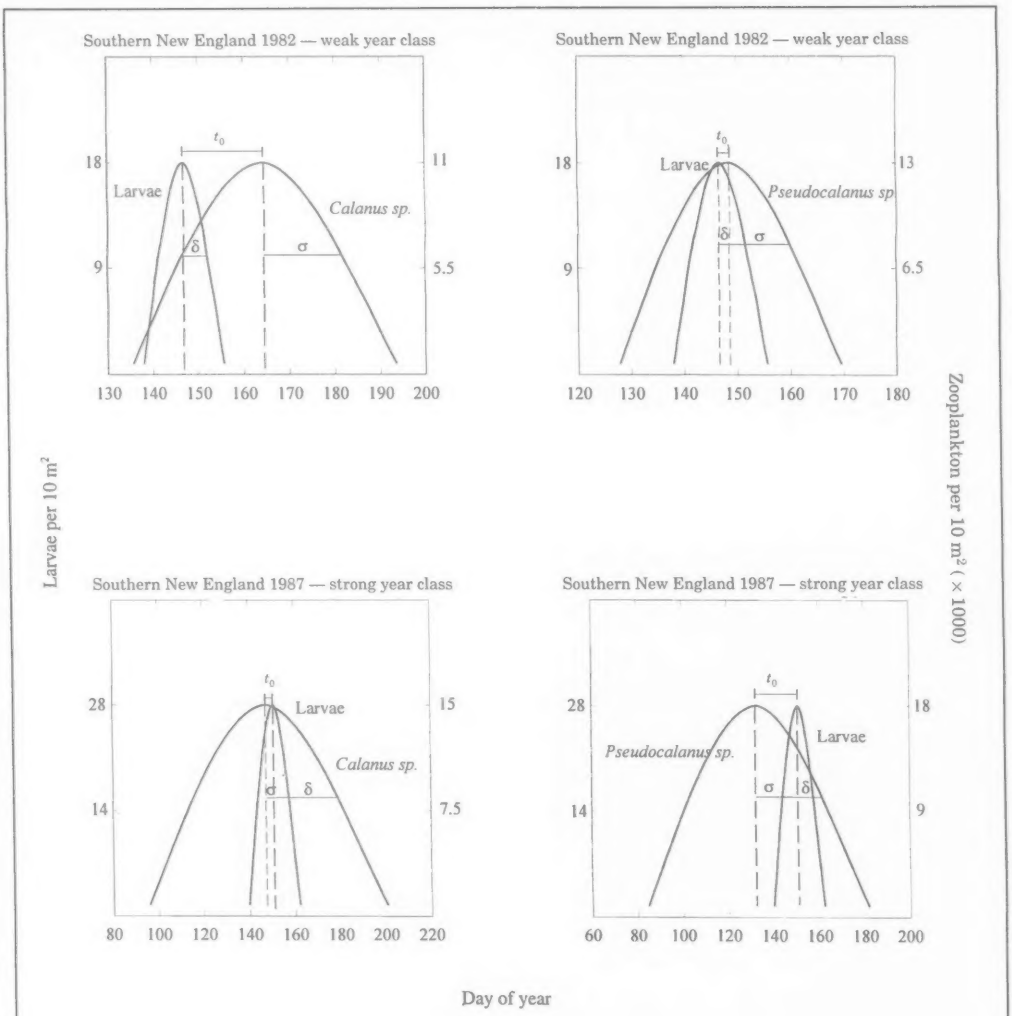

Figure 4

The match or mismatch relationship between yellowtail larvae, *Calanus* sp., and *Pseudocalanus* sp. in Southern New England during the year classes 1982 and 1987.

yellowtail larvae and *Pseudocalanus* sp. were examined for each subarea. In both subareas the strong year classes (1980, 1987 SNE; 1980, 1977 GB) were consistently positioned in ranges of t_0 less than zero. The extreme differences in predator and prey peaks frequently reflected the location of poorer year classes (1982, 1986 for both SNE and GB). Unexpectedly, these year classes normally occurred when predator and prey timing was equal to or greater than zero.

Although not statistically significant, the Spearman's rank-order correlation between predator-prey overlap and larval abundance suggested a possible relationship between recruitment variability and the predator-prey pairs, especially for the combination of larvae and *Calanus* sp. in SNE (Table 1).

Year-to-year variability in peaks of predator and prey abundance

As expected, the greatest anomaly in timing for three of the four predator-prey pairs occurred during the 1982 year class. The large difference in timing between predator and prey was reflected in the contour plot of larvae and zooplankton during 1982 (Fig. 7). There was a mismatch in timing between yellowtail flounder and *Calanus* sp. in GB and between yellowtail flounder and *Pseudocala-*

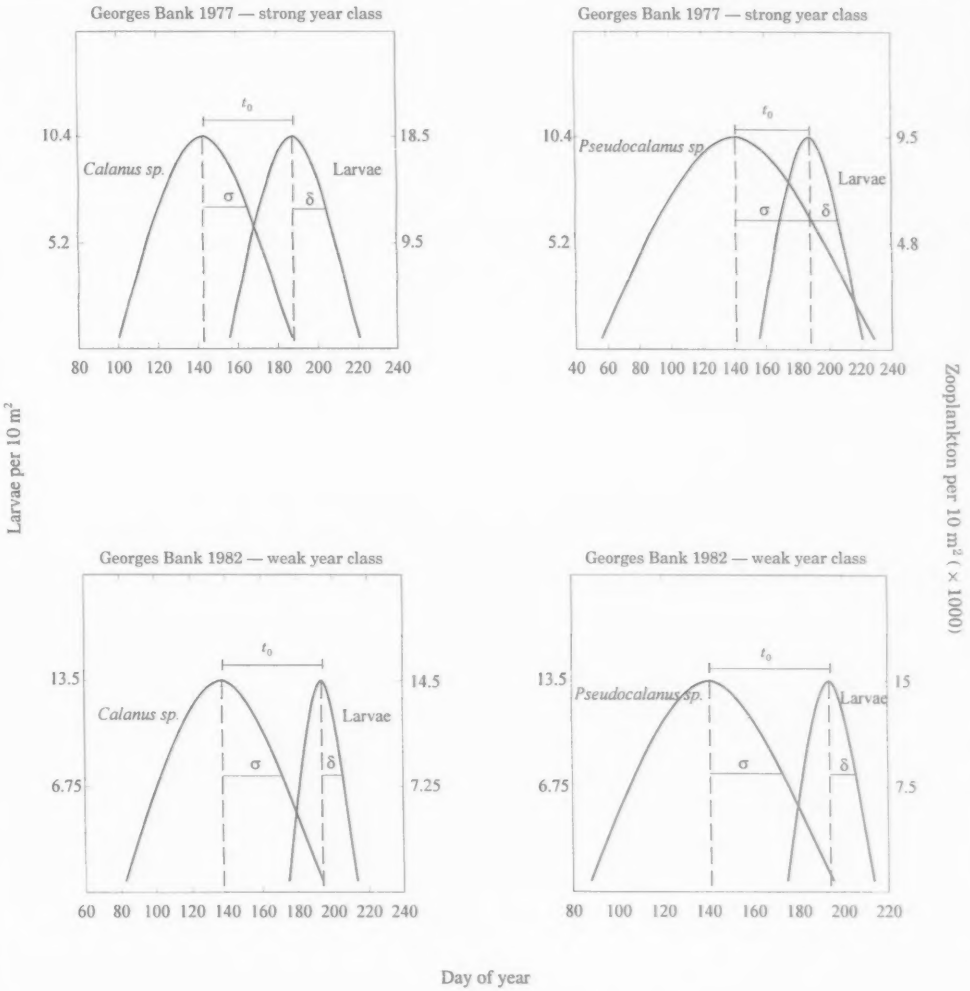

Figure 5

The match or mismatch relationship between yellowtail larvae, *Calanus* sp., and *Pseudocalanus* sp. in Georges Bank during the year classes 1977 and 1982.

nus sp. in SNE. Neither predator-prey pair was synchronous. In GB the yellowtail flounder larvae and *Calanus* sp. did not match in time or space. The zooplankton population appeared strong but the spawning of yellowtail flounder occurred during different times, creating low overlap between the two species. Years with the lowest anomalies in timing were 1984 and 1986 for GB and years 1977, 1980, 1986, and 1987 for SNE.

This study relied on extensive data for yellowtail flounder and zooplankton abundances in SNE and GB to test general predictions of the match-mismatch hypothesis. In general no strong support was found for this hypothesis. High overlap between zooplankton and yellowtail flounder abundances did not necessarily result in strong yellowtail flounder year classes, and some of the strongest year classes occurred when overlap was low.

Annual timing of spawning and production cycles from larvae and zooplankton prey (Table 2) also revealed variations between subareas. The spawning production for yellowtail flounder peaked earlier in the more southern subarea SNE than in GB, for all years excluding 1984. Similar results occurred in the production of *Pseudocalanus* sp., with the majority of first peaks cited in SNE for all years except 1978 and 1982. However, opposite patterns were observed for *Calanus* sp. production. Production cycles peaked first in seven of the eleven years in the

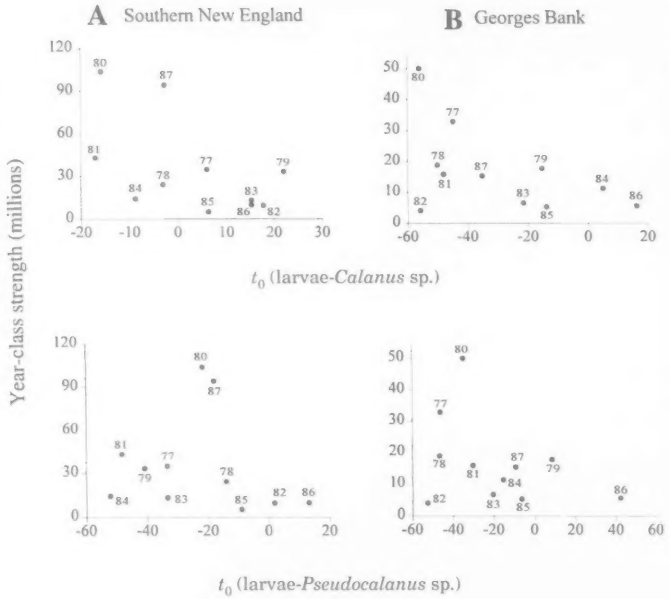

Figure 6

The relationship between peaks in predator-prey combinations and year-class strength for subareas Southern New England and Georges Bank during the years 1977–87.

Table 1

Spearman's rank-order correlation coefficients of predator-prey combinations (t_0) for subareas Southern New England (SNE) and Georges Bank (GB) during the 1977–87 time period.

Subarea	Predator-prey combination	r^2	$P>F$
SNE	larvae-*Calanus* sp.	–0.31	0.077
SNE	larvae-*Pseudocalanus* sp.	–0.21	0.160
GB	larvae-*Calanus* sp.	–0.20	0.170
GB	larvae-*Pseudocalanus* sp.	–0.07	0.417

GB subarea; the exceptions were the years 1984 through 1987. The mean differences in peaks for all years was 22.5 for larvae, 26.6 for *Pseudocalanus* sp. and –9.8 for *Calanus* sp.

Although this eleven-year study did reveal some possible relationships between predator and prey, there was no clear demonstration of a match or mismatch for strong or weak year classes. Results from this study were unable to conclude if high or low ratios between predator and prey abundance could determine or even predict the growth and survival of first-feeding larvae and their ultimate year-class success. Questions for future research should include 1) stomach-content analyses of larvae to determine prey, 2) incorporation of abiotic influences, and 3) sampling at a much smaller spatial scale. These additional features would increase the feeding success and growth rate estimation of young yellowtail flounder.

Acknowledgments

This note is dedicated to John B. Pearce in gratitude for his years of service and dedication to the field of fisheries science. He continues to be an inspiration to us all. I would like to thank Peter Berrien and Jay O'Reilly for their knowledge of and assistance in contouring. I would also like to thank Carol Meise for her help and suggestions with the zooplankton data set and especially thank the many people who participated in the MARMAP sampling program: all scientists and crew members aboard the research vessels who worked to collect and process samples during numerous uncertain conditions are gratefully acknowledged. I thank Michael Fogarty, Saran Twombly, William H. Krueger, and Jeremy Collie for their encouragement, review, and helpful suggestions. I also thank Wallace Morse, David Mountain, and John Boreman for insightful technical and policy reviews. Ransom A. Myers and an anonymous reviewer graciously provided helpful comments and suggestions.

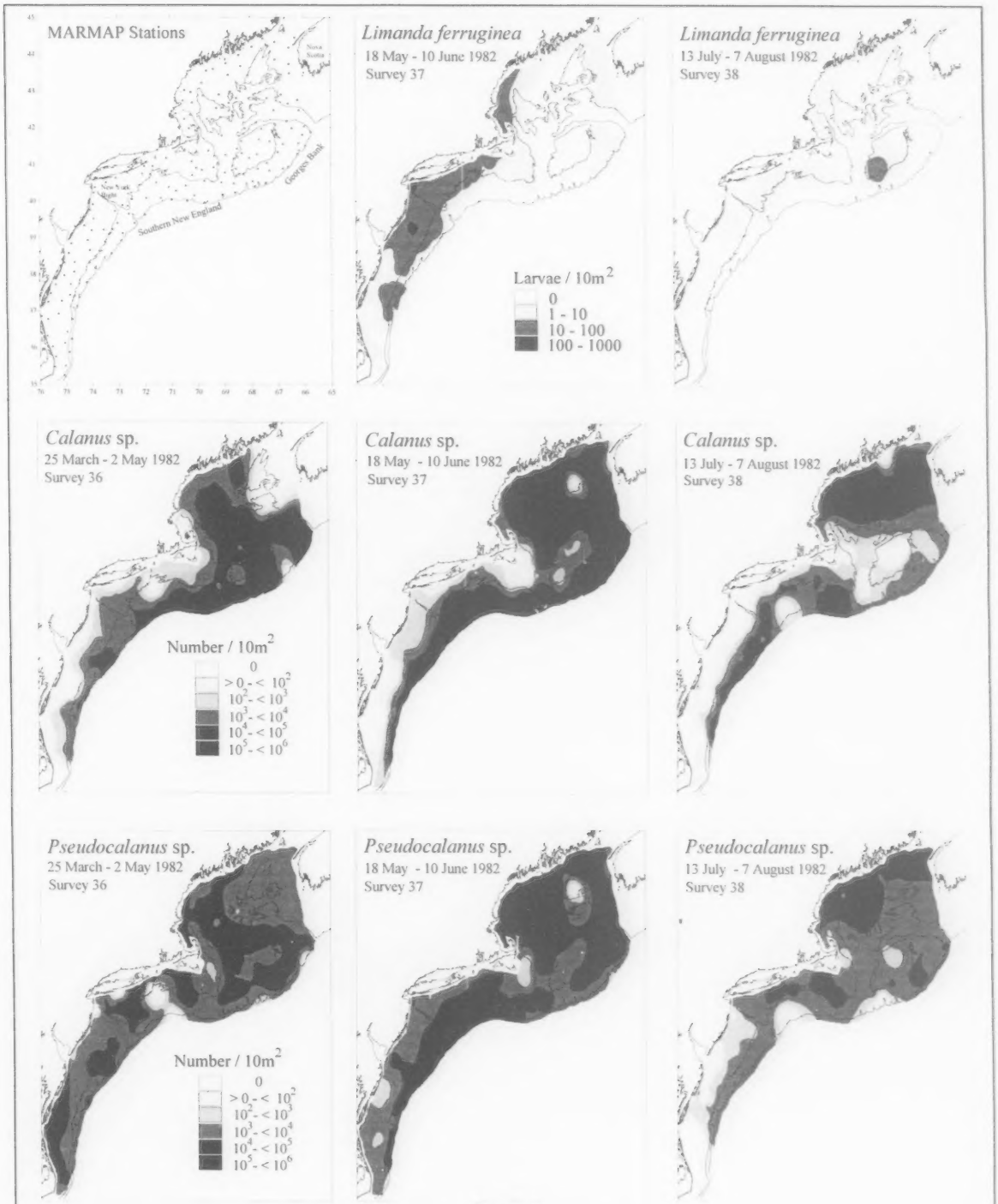

Figure 7

Distribution and abundance of predator *Limanda ferruginea*, and prey *Calanus* sp. and *Pseudocalanus* sp. during the production months of 1982.

Table 2

Mean dates of peak occurrence between spawning and production for yellowtail larvae and zooplankton. C – L = the difference between *Calanus* sp. (C) and larvae (L); and P – L = the difference between *Pseudocalanus* sp. (P) and larvae. (Values in bold were omitted from some parts of the analyses). SNE = Southern New England; GB = Georges Bank.

		Mean numeric date (Julian calendar)			t_0	
Subarea	Year	Yellowtail	*Calanus* sp.	*Pseudocalanus* sp.	C – L	P – L
SNE	1977	142.165	148.283	108.849	6.118	–33.316
	1978	**163.409**	**160.381**	**149.433**	**–3.028**	**–13.976**
	1979	**157.900**	**180.044**	**117.218**	**22.144**	**–40.682**
	1980	165.692	149.971	144.097	–15.721	–21.595
	1981	162.881	145.877	114.694	–17.004	–48.187
	1982	146.877	164.653	148.749	17.776	1.872
	1983	156.263	171.619	123.027	15.356	–33.236
	1984	**167.729**	**158.964**	**115.622**	**–8.765**	**–52.107**
	1985	**145.375**	**151.724**	**136.489**	**6.349**	**–8.886**
	1986	146.906	162.182	160.195	15.276	13.289
	1987	151.111	148.470	133.289	–2.641	–17.822
GB	1977	188.486	143.828	142.521	–44.658	–45.965
	1978	**190.935**	**141.003**	**144.407**	**–49.932**	**–46.528**
	1979	**158.285**	**143.063**	**167.135**	**–15.222**	**8.850**
	1980	198.189	142.306	163.603	–55.883	–34.586
	1981	173.270	125.278	143.250	–47.992	–30.020
	1982	194.324	138.514	141.743	–55.810	–52.581
	1983	**168.289**	**146.770**	**148.058**	**–21.519**	**–20.231**
	1984	162.345	167.399	147.164	5.054	–15.181
	1985	**171.862**	**157.967**	**165.720**	**–13.895**	**–6.142**
	1986	158.822	175.171	201.425	16.349	42.603
	1987	**188.463**	**153.322**	**179.525**	**–35.141**	**–8.938**

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Onset of association behavior in striped jack, *Pseudocaranx dentex*, in relation to floating objects

Reiji Masuda
Fisheries Research Station
Kyoto University
Nagahama, Maizuru
Kyoto 625-0086, Japan
E-mail address: reiji@kais.kyoto-u.ac.jp

Katsumi Tsukamoto
Ocean Research Institute
University of Tokyo,
1-15-1, Minamidai Nakano
Tokyo 164-8639, Japan

Many marine and freshwater species associate with floating objects (flotsam) during some period of their life history (Senta, 1965; Hunter and Mitchell, 1967; Kingsford, 1993). This association behavior is well known among fishermen, who often choose flotsam-associated schools (Yabe and Mori, 1950; Greenblatt, 1979). Among a wide range of taxa collected in association with flotsam, the Carangidae is one of the most frequently observed groups (Hunter and Mitchell, 1967; Kingsford, 1993; Clarke and Aeby, 1998). The association behavior of carangid fishes has been used by fishermen in Asia. "Payaw" in the Philippines is a flotsam made of bamboo and attracts many species of Carangidae (Ibrahim et al., 1990). Juvenile yellowtail, *Seriola quinqueradiata*, are collected by Japanese fishermen by surrounding drift algae with a small scoop net. These fish are then raised in cages as a net-pen culture (Senta, 1965; Sakakura and Tsukamoto, 1997). Presently, a new sea ranching project is being developed, in which artificially reared juvenile striped jack, *Pseudocaranx dentex*, are released at a floating platform where they naturally aggregate. There they are fed and harvested after growth (Masuda and Tsukamoto, 1998a).

The importance of this association behavior from the perspective of fishery ecology has generated a great deal of field research and experimental work. Hunter and Mitchell (1967) showed that large flotsam attracts more fish than smaller flotsam, and fish associating with flotsam tend to have darker body color, compared with the silvery color of those that are not attracted (Hunter and Mitchell, 1968). Using tag and release techniques, Ibrahim et al. (1990) demonstrated that fish released as far as 180 m from flotsam will swim back to their place of capture, suggesting that these fish can learn the topography of the region surrounding the float. Much ecological research has been conducted with the assumption that floating objects, especially drift algae, are an important habitat for juveniles (reviewed by Kingsford, 1993). Although a considerable amount of field-based work exists, little research has been conducted on the developmental aspects of association behavior in the laboratory.

The ontogenetic changes in association behavior in striped jack, *Pseudocaranx dentex*, were therefore studied with hatchery-raised larvae and juveniles. Possible sensory mechanisms underlying association behavior were examined by comparing four different types of flotsam conditions (transparent flotsam, gray flotsam, shadow flotsam, and no flotsam [control]).

Materials and methods

Two batches of fish were used in our experiments: one hatched on 22 February 1994, the other on 28 March 1994, both at the Komame Branch of the Japan Sea-Farming Association (JASFA). These batches of fish were transferred to the Kamiura Branch of JASFA on the next day. Fish were reared in 150-m^3 concrete tanks on a routine diet of rotifers and *Artemia* nauplii, and formula diet (Masuda and Tsukamoto, 1996). Eight different stages of fish were used in the experiments ranging from 5.5 mm (20 days) to 28 mm (56 days) in mean total length (Table 1). Because large variations in growth occurred in the hatchery, the medium-size fish were selected for each age group, except for the 21-mm fish. The 21-mm fish (54 days) were the smallest group of those hatched on 22 February.

Four different types of flotsam were created in 30-liter polycarbonate tanks with water depths of 25 cm (ca. 26 liters). These were

1 Transparent flotsam: a transparent acrylic pipe (60 mm in outer diameter, 5 mm thickness) cut to 250 mm in length and covered by a transparent circular plate (5 mm thickness) on the bottom. This was filled with water and suspended from the ceiling by fishing line, the height adjusted so that 150 mm of the pipe was in the water (Fig. 1A). The experimental tank was marked into four sections, and the flotsam was located at the center of one randomly chosen section.
2 Gray flotsam: an opaque gray PVC pipe and plate of identical size to that used in type 1 and suspended in the same way (Fig. 1B). This arrangement provided stronger visual stimulus than that provided in type 1.
3 Shadow flotsam: a gray circular opaque PVC plate (60 mm in diameter, 5 mm thickness) was suspended from the ceiling, so that the bottom of the plate was about 5 mm above the water surface. This created a shadow on the water surface, but not on the bottom of the tank (Fig. 1C).
4 No flotsam (control) (Fig. 1D).

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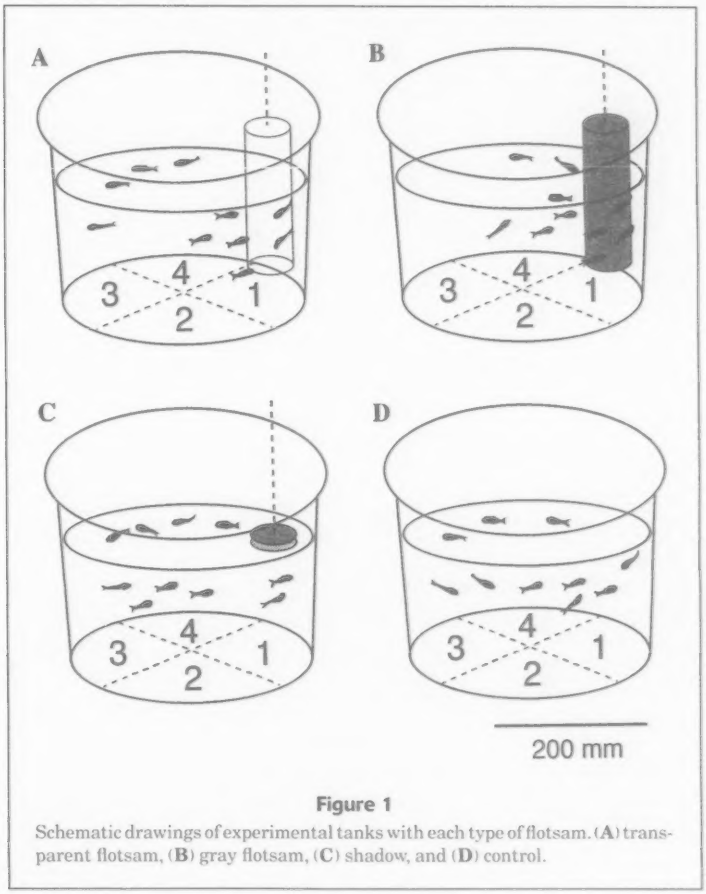

Figure 1

Schematic drawings of experimental tanks with each type of flotsam. (**A**) transparent flotsam, (**B**) gray flotsam, (**C**) shadow, and (**D**) control.

Carangid fish juveniles are commonly seen associated with floating and underwater objects, such as air tubes and vinyl bags, both in hatchery tanks and natural waters (Tachihara et al. 1993). Therefore acrylic and PVC pipes were suitable representative materials for use in examining the developmental changes of association behavior. We observed only horizontal distributions as an index of association behavior because in hatchery tanks, larvae and early juveniles of striped jack usually occur in the upper 30 cm of the water column.

All treatments were triplicated (twelve 30-liter tanks were used in total) and the location of the same type of flotsam was changed among triplicates. Experiments were conducted in an indoor facility and all tanks were placed in a water bath that was strongly aerated. Water temperature in each tank was maintained at hatchery levels (22.5°C). A photoperiod of 8 h light and 16 h dark was provided with 12 halogen illumination lights set above the tanks (light: 08:30–16:30 h). With this lighting, the light intensity at the surface of tanks was 0.01–0.05 lux at 20:00 h, lower than 0.01 lux between 00:00 and 04:00 h, 260–1000 lux at 08:00 h, and 17,000–24,000 lux at 12:00 and 16:00 h.

Table 1

Age, total length (mean ±SD), and hatching batch (+) of *Pseudocaranx dentex* used in the experiment.

		Batch	
Age (days)	TL (mm)	22 Feb	28 Mar 1994
20	5.5 ±0.5		+
27	8.8 ±0.9		+
30	10.3 ±1.1		+
31	11.9 ±2.4	+	
35	14.9 ±1.5		+
36	19.7 ±1.9	+	
54	21.0 ±1.8	+	
56	28.4 ±2.7	+	

At 20:00 h, fish were transferred from the hatchery tank to the 12 experimental tanks and ten fish were introduced into each tank (120 fish in total). Observations were con-

ducted immediately after introduction and once every 4 h over the following 24 h. For 10 mm, 15 mm, 21 mm, and 28 mm fish, observations were also made 36 h after introduction. During each observation period, the number of fish in each section of the tank was counted. At night time (20:00, 00:00 and 04:00 h), infrared illumination aided observation. At each observation, counts were repeated five times for each tank at approximately 5-min intervals. The average number of fish in each section with a flotsam was calculated and then divided by the total number of fish (n=10). This value, defined as the association ratio, would be 1.0 if fish associated strongly to the object and would be 0.25 with random movement or distribution. In the control treatment, the number of fish in the southeast, southwest, or northwest quadrants was counted from the triplicated tanks, respectively. The average value of these three tanks was used as a control. Total lengths of all the fish were measured after the experiment.

Association ratios were compared for each type of flotsam for each time of observation. Because association ratios deviated from normal distribution, we applied arcsine transformation (p'=arcsin$\sqrt{p}$; Zar, 1996). The resultant data showed nearly normal distribution. One-way ANOVA was then applied followed by Scheffé's test as a *post hoc* test (Zar, 1996; Abacus Concepts, Inc., 1992). We considered an association ratio higher than the control (P<0.05, Scheffé's test) to be evidence of association behavior with that flotsam.

Results

In 5.5-mm, 8.8-mm, and 10-mm fish, no association behavior was observed with any types of flotsam, and the average association ratios were always near 0.25 (Fig. 2, A–C). At 12 mm, the first significant association behavior was observed both with transparent and gray objects (Fig. 2D; P<0.05). Association ratios did not differ significantly between these two object types at this stage (P>0.2). At 15 mm, association behavior was not obvious, perhaps because the fish swam around in the tank restlessly in this particular trial, both in test and control groups. At 20 mm, association was again obvious and the association ratio to the gray pipe tended to be higher than that to the transparent pipe (P=0.013 at 20:00 h on the second day, Fig. 2F). Association behavior was especially strong at night, and some individuals almost touched the transparent and gray pipes (Fig. 3). In most cases it took at least 12 h for fish to show an association behavior in the experimental tank, but 21-mm fish showed an association with gray objects immediately after they were introduced to the tank. At 28 mm, an association with transparent and gray pipes was positive, but the association ratio tended to be slightly less than fish at 20 mm and 21 mm. No association behavior with shadows was observed at any life-history stage of the fish.

Association ratios after 12 h and 24 h in the experiment (12:00 h and 20:00 h on the second day) were plotted against the total length of each fish (Fig. 4), showing that striped jack begin association behavior at 12 mm in TL with both transparent and gray objects.

Discussion

Accurate observation of association behavior can suffer from biases attributed to other behavior and taxis. For example, striped jack show strong phototaxis from 3.5 mm TL and rheotaxis from 4.5 mm TL (Masuda and Tsukamoto, 1996). In the present study these potential confounding factors were prevented by illuminating the tanks strongly from above and by using tanks without currents. This procedure was apparently successful because most fish smaller than 10 mm distributed themselves about equally in the experimental tanks (Fig. 2, A–C). Striped jack also exhibit schooling behavior from about 16 mm (Masuda and Tsukamoto, 1998b) which may have contributed to the fluctuating association ratio values with 15-mm or larger fish in the control tanks (Fig. 2, E and F).

Small tank size (30 liters) used in this experiment may have affected the results because the fish may have considered a tank wall as a structure with which to associate. However, fish apparently preferred the pipe to the tank wall and associated closely with it (Fig. 3). Strong aeration outside tanks in the water bath might have minimized their association to the tank wall. The limited swimming ability and shortsightedness of the larvae and juveniles also helped to reduce the effect of the tank wall.

Our results indicate that striped jack first started to show association behavior at 12 mm TL. Hunter and Mitchell (1967) reported six species of carangid fish juveniles associated with flotsam offshore Costa Rica, and their smallest sizes (given as standard lengths) were as follows: *Caranx caballus*: 9 mm; *C. hippos*: 16 mm; *Decapterus sp.*: 17 mm; *Elagatis bipinnulatus*: 11 mm; *Selar crumenophthalmus*: 15 mm; and *Seriola sp.*: 10 mm. From observation of hatchery tanks, Tachihara et al. (1993) reported that artificially reared greater amberjack, *Seriola dumerili*, larger than 11 mm standard length associate with objects. The smallest size of an flotsam-associating individual in natural waters may differ depending on species, area, season, and sampling methods. The smallest size (12 mm in TL) to associate with flotsam in our study was therefore consistent with field and hatchery observations of other carangid species.

We hypothesized that mechanical and visual stimuli may be cues for association behavior. No association with shadow flotsam was observed at any fish stages in our study, suggesting that shade is too weak a stimulus to evoke association behavior. At 12 mm, association behavior was observed to both transparent and gray flotsam, and in fish larger than 20 mm, association to gray flotsam was stronger. This finding suggests that in early juvenile stages, a mechanosensory system, as well as vision, may be involved in association behavior. Striped jack showed stronger association behavior in darkness than in light—a finding that seems to conflict with Gooding and Magnuson (1967) who found that residents of an experimental floating raft accumulate more rapidly by day than by night. In nature striped jack may find flotsam by vision during the daytime and maintain an association with it by a mechanosensory system during night. Floating structures may serve as feeding places, shelters from predation, and

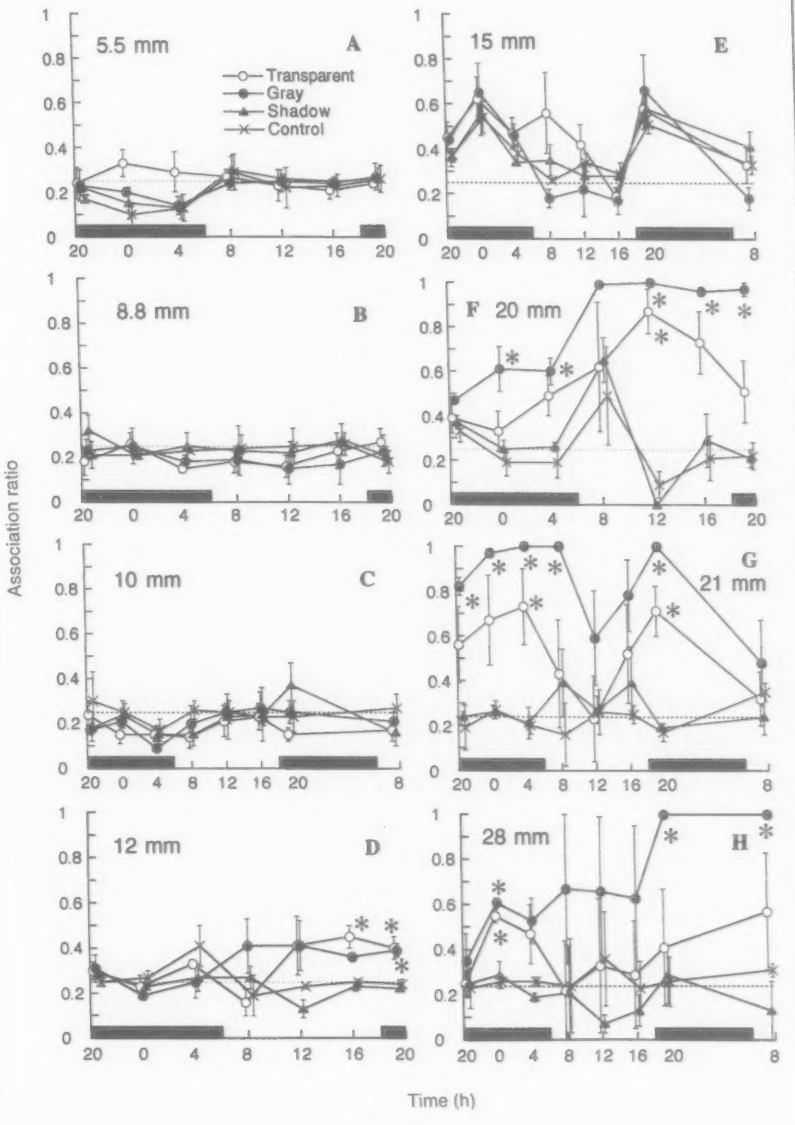

Figure 2

Association ratios for each type of flotsam in each stage. Each plot represents an average (±SE) of three tanks with the same type of flotsam. * shows significant difference between tests and controls ($P<0.05$; Scheffé's test). Expected value of random distribution (=0.25) is represented as a dotted line in each graph. Shaded bar corresponds with dark hours.

cues to migratory orientation (Hunter and Mitchell, 1967; Gooding and Magnuson, 1967; Kingsford, 1993). Flotsam may provide the first cue to finding conspecifics and to forming a school because association behavior may also be related to school formation and maintenance (Masuda and Tsukamoto, 1998b).

In conclusion, the association behavior of striped jack appeared at 12 mm and is probably dependent on a mechanosensory system, as well as vision. Association behavior may also help the development of schools and may provide transportation for migration. Environmental modifications that reduce flotsam, such as the removal of drift

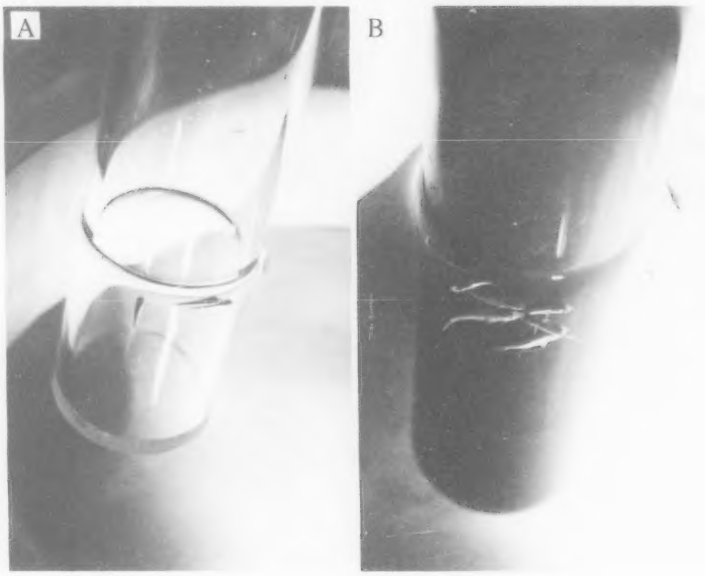

Figure 3

Typical association behavior of striped jack at night observed in 20-mm-TL juveniles: (**A**) transparent flotsam, (**B**) gray flotsam.

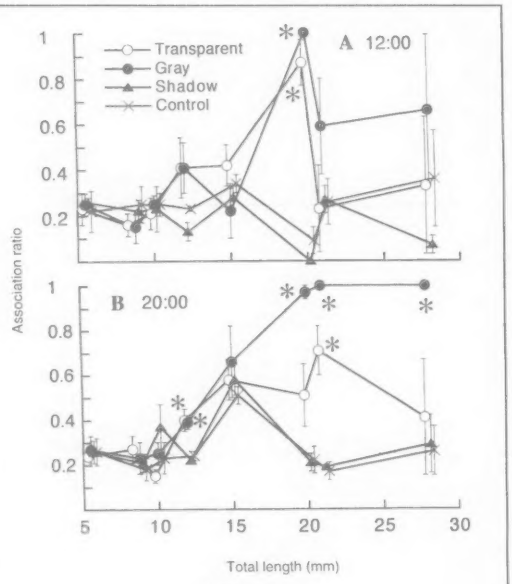

Figure 4

Onset of association behavior in the striped jack. Association ratios at 16 h (**A**) and 24 h (**B**) after starting experiments (12:00 and 20:00) were plotted against total length at each stage. * shows significant difference between tests and controls ($P<0.05$; Scheffé's test).

algae, may influence the recruitment of flotsam-associating species.

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The occurrence of the provisional Brazilian subspecies of spiny lobster (*Panulirus argus westonii*) in Florida waters*

Shane K. Sarver
Department of Biology
Black Hills State University
Spearfish, South Dakota 57799
E-mail address: ssarver@mystic.bhsu.edu

D. Wilson Freshwater
Center for Marine Science Research
7205 Wrightsville Avenue
Wilmington, North Carolina 28403

Patrick J. Walsh
Division of Marine Biology and Fisheries
Rosenstiel School of Marine and Atmospheric Science
University of Miami
Miami, Florida 33149

The Caribbean spiny lobster, *Panulirus argus*, is distributed from Brazil throughout the Caribbean and the Gulf of Mexico to approximately North Carolina and Bermuda (Holthius, 1991). It supports major commercial fisheries in Florida, the Caribbean and Brazil. Commercially, *P. argus* is especially important to the state of Florida, where the spiny lobster fishery ranks second only to shrimp in terms of economic value. There is also a significant recreational fishery for *P. argus*, particularly in Florida. A number of studies have been initiated to gather information to manage the lobster resource carefully.

Several studies have used genetic techniques to examine population-level patterns of differentiation to delineate reproductively isolated stocks of *P. argus*. Evidence of the stock structure of spiny lobster populations could then be used to implement more effective fishery management plans. These studies have provided somewhat ambiguous results. Using allozymes, Menzies and Kerrigan (1979) and Menzies (1981) provided some evidence for genetic differences among populations, but more recent studies using restriction fragment length polymorphism (RFLP) analysis of mitochondrial DNA have suggested little evidence for genetic differences among Caribbean populations of *P. argus* (Silberman et al., 1994a, 1994b). Analysis of mtDNA RFLPs have revealed suprisingly high levels of diversity among individuals, and several individuals were diverged at levels not usually seen within a species. Because previous studies did not include populations from Brazil, Sarver et al. (1998) compared *P. argus* from Caribbean locations with *P. argus* from Brazil. Using DNA sequence analysis of two mitochondrial genes, Sarver et al. (1998) found high levels of sequence divergence between Caribbean and Brazilian *P. argus*. The levels of nucleotide sequence divergence were greater than that seen between recognized species of *Panulirus*. In addition, there are striking color differences between Caribbean and Brazilian *P. argus*. As a result of these findings Sarver et al. (1998) suggested provisional recognition of two subspecies of *P. argus* (*P. argus argus* in the Caribbean and *P. argus westonii* in Brazil) until a formal taxonomic revision could be done.

The results from these studies, which suggest that *P. argus* in Brazil are genetically and taxonomically distinct from their Caribbean counterparts, have raised questions about the status of the three genetically distinct spiny lobsters reported by Silberman et al. (1994a) in their original survey of mtDNA diversity of Caribbean *P. argus*. This is significant because two of these spiny lobsters found in Silberman et al. (1994a) were caught off the coast of Miami, Florida. Our study uses DNA sequence analysis to identify the three genetically distinct spiny lobsters observed by Silberman et al. (1994a) as the Brazilian form of *P. argus* (provisionally recognized as *P. argus westonii*, in Sarver et al., 1998).

Materials and methods

DNA samples were obtained from the samples examined by Silberman et al. (1994a). Caribbean *Panulirus argus* samples were randomly selected from the samples examined by Silberman et al. (1994a). Samples from Brazil were collected near the Rio Grande do Norte region of Brazil. Tissue samples of *Panulirus argus* from Brazil were frozen prior to DNA isolation. Standard phenol or chloroform DNA extraction techniques were used for DNA isolation (Hillis et al., 1990). A region of the mitochondrial 16S rRNA gene was amplified by the polymerase chain reaction (PCR) by using primers 16Sar and 16Sbr given in Palumbi et al.[1] PCR products were then purified and used as templates for DNA sequencing by using the ΔTaq cycle sequencing kit (U.S. Biochemical Corp., Cleveland, OH). Cycle sequencing reactions were performed by using γ-^{33}P-dATP end-

* Contribution 221 of the Center for Marine Science Research, Wilmington, NC 28403.

[1] Palumbi, S. R., A Martin, S. Romano, W. O. McMillan, L. Stice, and G. Grabowski. 1991. A simple fools guide to PCR, vers. 2.0. Special publication of the University of Hawaii Department of Zoology and Kewalo Marine Laboratory, 46 p. Department of Zoology and Kewalo Marine Laboratory, Univ. Hawaii, Honolulu, HI 96822.

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labeled primers. All sequences were determined in both directions.

Aligned DNA sequence data included 441 sites. Distance and parsimony analyses of the aligned DNA sequences were done with PAUP (Swofford, 1998). Three separate distance calculations were made: uncorrected mean, Jukes-Cantor (Jukes and Cantor, 1969), and Kimura 2-parameter (Kimura, 1980) distances. Neighbor-joining trees (Saitou and Nei, 1987) were generated by using all three distance measures. Parsimony trees were produced by using branch and bound searches. Sites coded as gaps were treated either as missing, or as a fifth character state. The mitochondrial 16S rDNA sequences were aligned by using the SeqPup DNA analysis program (Gilbert[2]). Support for nodes of both parsimony and distance trees was assessed by calculating bootstrap proportion (BP) values (Felsenstein, 1985) from 1000 replicate searches by using the same tree building methods used to produce the trees. *Scyllarides nodifer* (Stimpson) (Decapoda, Scyllaridae) was used as an outgroup for phylogenetic analyses.

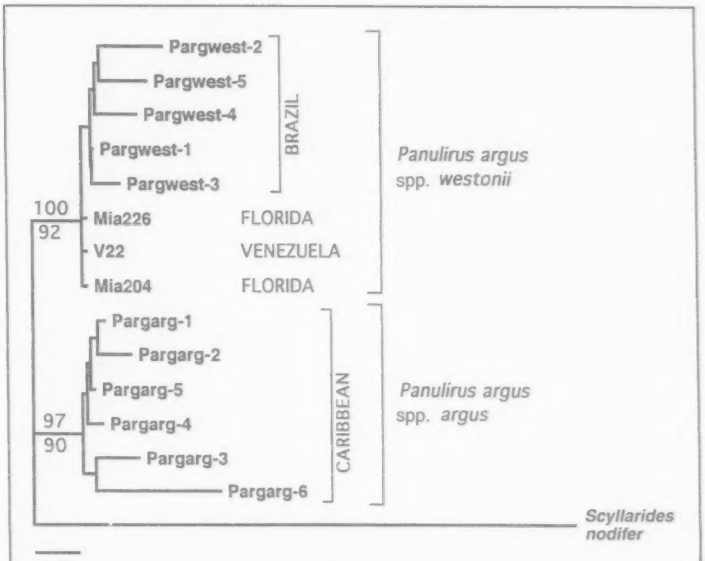

Figure 1

Neighbor joining tree derived from the Kimura two-parameter distances calculated from partial mitochondrial 16S rDNA data for 14 *Panulirus argus* and *Scyllarides nodifer* samples. Bootstrap values calculated from the distance analysis are shown above and bootstrap values calculated from parsimony analysis are shown below strongly supported branches.

Results

The mitochondrial 16S rDNA region analyzed in our study included 441 aligned nucleotide positions. In addition to single base differences, the complete aligned data set included 19 presumptive insertion or deletion mutations (indels) of 1–5 bases in length. The majority of indels involved only one base (13 of 19) and only six were potentially informative.

Regardless of the type of distance calculation, there was little variation in the outcome of the different distance calculations (less than 1%). Results from an analysis with a Kimura 2-parameter model yielded distance values ranging from 5.9% to 15.1% between the Caribbean and Brazilian subspecies of *Panulirus argus* (*P. argus argus* and *P. argus westonii* respectively). For the three genetically distinct Caribbean *P. argus* from Silberman et al. (1994a), sequence divergence estimates indicated closer affinities to Brazilian *P. argus* (2.6%) than to the Caribbean *P. argus* (7.4%).

Phylogenetic analysis of Brazilian, Caribbean and the three divergent Caribbean *P. argus* indicated a tree topology that places the three divergent Caribbean samples of *P. argus* in the Brazilian clade (Fig. 1). This basic tree topology is strongly supported regardless of the method of phylogenetic analysis.

Discussion

Traditionally, *Panulirus argus* has been thought to be distributed from North Carolina in the western Atlantic, throughout the Caribbean to Rio de Janeiro, Brazil. Sarver et al. (1998) presented data that questioned the taxonomic status of *P. argus*. DNA sequence data and morphological differences suggest that populations of *P. argus* from Brazil are genetically distinct from Caribbean populations and that the level of divergence is equivalent to the levels of divergence seen between recognized species of *Panulirus*. As a result they suggested formally recognizing two genetic forms of *P. argus* and have recommended provisional subspecific status: *P. argus argus* (Caribbean) and *P. argus westonii* (Brazil) until a formal taxonomic revision can be done. The occurrence of cryptic species in *Panulirus* is not restricted to *P. argus*. A similar situation exists in *P. longipes*, where there appears to be at least four recognizable forms of uncertain taxonomic status (George, 1972; Sekiguchi, 1991; Chan and Chu, 1996). *Panulirus homarus* has also been broken into three geographic forms that are given the rank of subspecies (Berry, 1974).

We can only speculate on the events that led to this distribution of the two *P. argus* subspecies. During the late Miocene Epoch, a *P. argus* ancestor may have occupied the North Atlantic and as Africa and South America moved apart as a result of continental drift, habitat became available for *P. argus* along the South America coast. These pop-

[2] Gilbert, D. G. 1996. SeqPup biosequence editor and analysis application, vers. 0.6f. Department of Biology, Univ. Indiana, Bloomington, IN 47405.

ulations then could have been isolated as a result of the Andes uplift during the Pliocene Epoch, which altered the pattern of the runoff and changed the course of the major rivers of the Amazon basin. Runoff from the Amazon basin continues to act as a barrier to larval migration and effectively separates Caribbean *P. argus argus* and Brazilian *P. argus westonii*. Levels of nucleotide sequence diversity observed between *P. argus argus* and *P. argus westonii* are compatible with this hypothesis.

Low numbers of the Brazilian form of *P. argus* in the Caribbean may result from rare migration events or the co-occurrence of both forms in the Caribbean. Long-range dispersal of larvae is especially well developed in *P. argus*. The complex life cycle of spiny lobsters is characterized by a protracted larval phase (the phyllosome) which can last from several months to two years and can result in prolonged transport by ocean currents (Sims and Ingle, 1967). Postlarval recruitment for some species of *Panulirus* has been associated with variation in large-scale oceanic processes (Phillips and Pearce, 1997). El niño-like events could alter the current regimes and allow some of the Brazilian forms of *P. argus* to escape into the Caribbean. Episodic recruitment events could also explain the occurrence of *Panulirus laevicauda* in the Caribbean. *Panulirus laevicauda* is abundant in Brazilian waters but is only rarely found in the Caribbean. Evidence for sporadic recruitment of *P. laevicauda* in the Caribbean was reported by Moore (1962), who noted finding a single specimen of *P. laevicauda* near Palm Beach, Florida, during 1949. Later that same year, *P. laevicauda* was reported to be nearly as abundant as *P. argus*, but in the following three years, no *P. laevicauda* were found at this location.

Occurrence of the Brazilian form of *P. argus* in Florida waters raises a number of interesting biological questions. Given the morphological differences and the high degree of genetic differentiation between Caribbean and Brazilian *P. argus*, are they capable of interbreeding? It could be possible that the existence of the Brazilian *P. argus* mtDNA haplotype in the Caribbean could be the consequence of leakage of the Brazilian *P. argus* mtDNA genome across the species boundary as a result of interbreeding. Because most of the research conducted with *P. argus* has been done with Caribbean *P. argus*, do the two forms of *P. argus* differ biologically? George (1997) considers Brazilian and Caribbean *P. argus* to be distinct ecologically and has suggested that *P. argus* is likely a complex of two species. Knowledge of the occurrence of *P. argus argus* in Brazilian waters is lacking. Taxonomic ambiguity surrounding *P. argus* is a concern because of its commercial importance. For example, Florida regulations currently prohibit the transportation or sale of imported *P. argus* during the time of year when the fishery is closed in Florida. If two species become recognized, under the present regulations, *Panulirus* from Brazil could be sold year round in Florida. If there are indeed two species of *P. argus* in Florida waters, as it appears there are, then fishery regulations will need to reflect this reclassification. Currently, fishery regulations apply to *Panulirus argus*, and all subspecies of spiny lobsters are subject to the same rules, but other species are not regulated.

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On comparison of growth curves: How do we test whether growth rates differ?

You-Gan Wang

CSIRO Mathematical and Information Sciences
P.O. Box 120
Cleveland
Queensland 4163, Australia
Present address: Department of Biostatistics
Harvard School of Public Health
655 Huntington Avenue
Boston, Massachusetts 02115
E-mail address: ygwang@hsph.harvard.edu

David A. Milton

CSIRO Marine Research
P.O. Box 120
Cleveland
Queensland 4163, Australia

Comparisons of growth rates of populations and species are important in fisheries science for a range of reasons that vary with the context of each study. Most studies of fish growth have focused on the practical issues of the most appropriate way of comparing growth rather than on recognizing that there are several methods for making these comparisons and that the conclusions will differ depending on the method chosen.

Francis (1996) discussed the problem of how to compare different growth rates or growth curves. He suggested six plausible ways of making a comparison and suggested that the rate at which the asymptotic size is approached was the most natural method of comparing growth (his method 6). He illustrated the differences between the methods by comparing von Bertalanffy growth equations that are based on fixed growth parameters and that assumed that growth parameters are known and there are no associated uncertainties. However, in practice, the growth parameters are often estimated, and therefore are random variables. Consequently, the corresponding growth curves are also subject to variations.

For comparison with Francis's work, we will assume that growth for a species is adequately described by the von Bertalanffy equation with $t_0 = 0$, as

$$L(t;\beta) = l_\infty (1 - e^{-kt}), \qquad (1)$$

in which $\beta = (k, l_\infty)$ are growth parameters.

Here $l(t)$ is the mean length at age t. If $\hat{\beta}_1$ and $\hat{\beta}_2$ are two estimates of β, how do we test whether the corresponding two growth curves are the same? The traditional way is to compare individual parameters and find out which ones are significantly different. However, the parameter estimates, l_∞ and k, are often strongly correlated (Kirkwood and Somers, 1984; Wang and Thomas, 1995). It may therefore be more appropriate to compare biological reference points (e.g. size at one year of age) rather than growth parameters in the models (Wang and Thomas, 1995). Growth comparisons may, in general, be classified into two types: within species and between species. In practice, the following comparisons may be of interest:

1 Comparison of the growth rates for the same species, say E, in which two sets of growth parameter estimates, $\hat{\beta}_1$ and $\hat{\beta}_2$, are obtained from different time periods, different areas or sexes.

2 Comparison of growth rates for two different species to see which one grows faster.

As mentioned earlier, Francis (1996) considered six methods for comparing growth. For the within-species comparison, it seems all six methods are valid. However, these methods compare different characteristics of growth and therefore may reach different conclusions. For example, if we obtain $\hat{\beta}_1 = (0.5,50)$ from area A and $\hat{\beta}_2 = (0.4,60)$ from area B, we would conclude that species E does not grow as large in area A as in area B and that the k value (rate at which the asymptotic length is approached) in area A is larger than that in area B.

For between-species comparisons, we agree with Francis (1996) that his method 6 (k value comparison) is probably the most appropriate, especially in the context of comparing growth between, for example, herring and orange roughy. However, in some cases, comparing absolute growth rates at age or length between species could be of practical interest.

For example, if you are interested in choosing one of two species of fish or crustacean to farm and these two species look alike and have the same commercial value, it is more economical to farm the faster-growing species to shorten the time taken to reach market size. In Australia, the tiger prawn *P. esculentus* has a larger k value than the very similar *P. semisulcatus* (Somers and Kirkwood 1991), but *P. semisulcatus* has the potential of reaching a commercial size sooner (Fig. 1). Therefore, we would conclude that *P. semisulcatus* grows faster than *P. esculentus* in this context, and a comparison based only on k values may be misleading.

Therefore, in this note we will extend Francis's theoretical study by developing procedures for establishing statistical hypotheses for the six methods and suggest test statistics for comparing growth curves. We will demonstrate the differences in conclusions that can occur among the methods with data on

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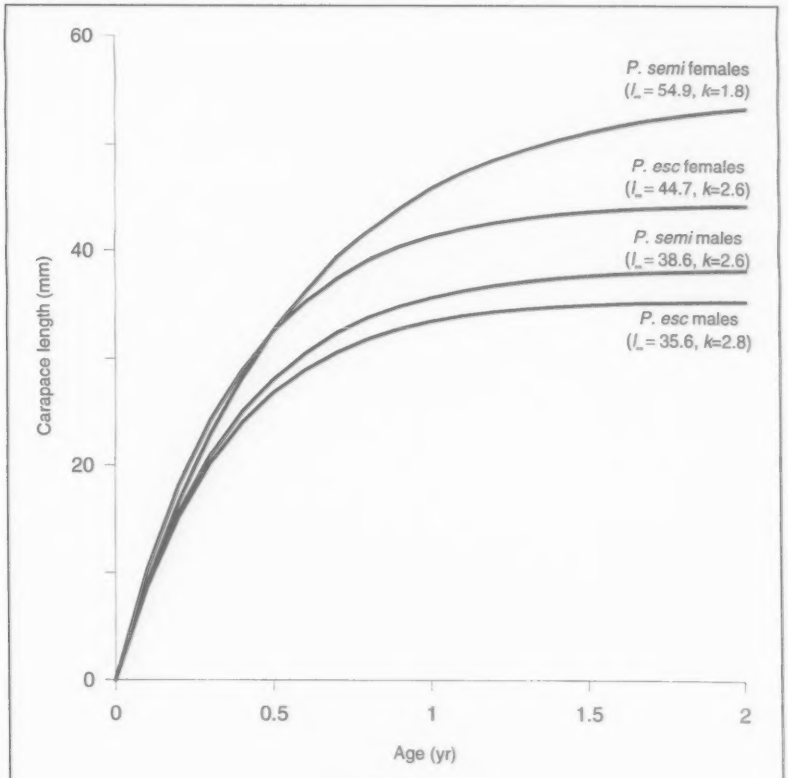

Figure 1

A plot of the von Bertalanffy growth curves for male and female *P. semisulcatus* (*P. semi*) and *P. esculentus* (*P. esc*) that are being compared by the six methods identified by Francis (1996).

growth rates of two species of tiger prawn (shrimp) from northern Australia.

Methods

Overall hypothesis tests on two sets of parameters

Suppose we are interested in testing the hypothesis that the underlying growth curves corresponding to the two sets of parameter estimates $\hat{\beta}_1 = (k_1, l_{\infty 1})$ and $\hat{\beta}_2 = (k_2, l_{\infty 2})$ are the same. According to the large-sample theory, it is quite reasonable in most cases to assume that $\hat{\beta}_1$ and $\hat{\beta}_2$ are normally distributed. To be general, we will allow $\hat{\beta}_1$ to be correlated with $\hat{\beta}_2$. In notation,

$$\begin{pmatrix} \hat{\beta}_1 \\ \hat{\beta}_2 \end{pmatrix} \approx N\left(\begin{pmatrix} \beta_1 \\ \beta_2 \end{pmatrix}, \begin{pmatrix} \Sigma_1 & \Sigma_{12} \\ \Sigma_{12} & \Sigma_2 \end{pmatrix} \right). \quad (1)$$

Note that if $\hat{\beta}_1$ and $\hat{\beta}_2$ are estimated from different data sets, they may be assumed to be independent, because both $\hat{\beta}_1$ and $\hat{\beta}_2$ are estimates and $\hat{\beta}_1 - \hat{\beta}_2$ is approximately multivariate normal. To test whether the two growth patterns determined by $\hat{\beta}_1$ and $\hat{\beta}_2$ are the same or not, we can use the generalised T^2-statistic (Anderson, 1971):

$$T^2 = (\hat{\beta}_1 - \hat{\beta}_2)' V^{-1} (\hat{\beta}_1 - \hat{\beta}_2), \quad (2)$$

in which V = the covariance of $\hat{\beta}_1 - \hat{\beta}_2$.

The distribution of the T^2-statistic is approximately chi-squared with 2 degrees of freedom, χ^2_2. If the significance level is α, the corresponding critical value is $\chi^2_2(\alpha)$.

In many cases, we are interested in the slope of the growth curve (growth rate) rather than the curve itself. For example, we may be interested in comparing the growth rate during a particular age interval. Owing to natural mortality or fishing mortality, the period outside of this age range may be of no practical interest. In this case, it is may be more appropriate to consider the growth patterns over a specified age or length range rather than the whole range, which would put more emphasis (weight) on the asymptotic length in the comparison.

Tests to compare two growth equations Let g be a growth function of (k, l_∞) that we are interested in comparing. Table 1 lists the six g functions corresponding to the six methods identified by Francis (1996). For a given function g, we will test $g(\beta_1) = g(\beta_2)$ versus $g(\beta_1) \neq g(\beta_2)$ or $g(\beta_1) > g(\beta_2)$, depending on the context. Standard normal tests may be used for a specified g function. The test will rely on the properties of $D \approx g(\hat{\beta}_1) - g(\hat{\beta}_2)$. Let $E(D)$ and $V(D)$ be the corresponding expectation and variance of D when β is the true parameter. Under the null hypothesis, $g(\beta_1) = g(\beta_2)$, and using standard Taylor series expansion, we can work out analytic expressions of $E(D)$ and $V(D)$. Some pooled estimates of β may be required to input to $E(D)$ and $V(D)$ to obtain approximate values of $E(D)$ and $V(D)$. We can obtain $E(D)$ from $Eg(\hat{\beta}_1) - Eg(\hat{\beta}_2)$ and

$$E\left(g(\hat{\beta})\right) \approx g(\beta) + \frac{1}{2}\left(f_{11}\sigma_{11}^2 + 2f_{12}\sigma_{12} + f_{22}\sigma_{22}^2\right), \quad (3)$$

in which f values are from the second derivative of g with respect to β (Table 1) and

$$\begin{pmatrix} \sigma_{11}^2 & \sigma_{12} \\ \sigma_{12} & \sigma_{22}^2 \end{pmatrix} = V(\hat{\beta}). \quad (4)$$

The variance of D can be obtained from

$$V(D) \approx X_1^T \Sigma_1 X_1 + X_2^T \Sigma_2 X_2 - 2X_1^T \Sigma_{12} X_2, \quad (5)$$

in which X_i = the gradient or first derivative of g_i (Table 1); and

Σ's = the components of the covariance defined earlier.

Note that the last term disappears if $\hat{\beta}_1$ and $\hat{\beta}_2$ are independent of each other. There are a few possible ways to obtain the approximate significance level, P. However, the most widely used method assumes D is normally distributed. Then we can use the z-test, which is based on the normal approximation for large sample sizes. For a one-sided test $g(\beta_1) = g(\beta_2)$ vs. $g(\beta_1) > g(\beta_2)$

$$P \approx 1 - \Phi\left(\frac{\hat{D}}{\sqrt{V(\hat{D})}} = \Phi\left(\frac{-\hat{D}}{\sqrt{V(\hat{D})}}\right)\right), \quad (6)$$

where Φ = the standard normal distribution function.

For a two-sided test, we have

$$P \approx 2\Phi\left(\frac{-\left|\hat{D}\right|}{\sqrt{V(\hat{D})}}\right). \quad (7)$$

If we are interested in the growth for a range of ages (t_{min}, t_{max}), or the sizes (l_{min}, l_{max}), we may consider the in-

Table 1

The six growth models $g(\beta)$ that correspond to methods of comparing mean growth of two species or populations in Francis (1996) and their first $X = \frac{dg}{d\beta}$ and second $F = \frac{d^2g}{d\beta^2}$ derivatives assuming $\beta \sim (\beta_0, \Sigma)$.

Method	$g(\beta)$	X	F
1 Comparison of lengths at each age	$g = l_\infty(1 - e^{-kt})$	$\begin{pmatrix} l_\infty t e^{-kt} \\ 1 - e^{-kt} \end{pmatrix}$	$\begin{pmatrix} -l_\infty t^2 e^{-kt} & te^{-kt} \\ te^{-kt} & 0 \end{pmatrix}$
2 Comparison of absolute growth rates at each age	$g = l_\infty k e^{-kt}$	$\begin{pmatrix} l_\infty e^{-kt}(1 - kt) \\ ke^{-kt} \end{pmatrix}$	$\begin{pmatrix} -(2 - kt)tl_\infty e^{-kt} & (1 - kt)e^{-kt} \\ (1 - kt)e^{-kt} & 0 \end{pmatrix}$
3 Comparison of absolute growth rates at each length	$g = (l_\infty - l)k$	$\begin{pmatrix} l_\infty - l \\ k \end{pmatrix}$	$\begin{pmatrix} 0 & 1 \\ 1 & 0 \end{pmatrix}$
4 Comparison of relative growth rates at each age	$g = \frac{ke^{-kt}}{1 - e^{-kt}}$	$\begin{pmatrix} \frac{1 - e^{-kt} - kt}{(1 - e^{-kt})^2} e^{-kt} \\ 0 \end{pmatrix}$	$\begin{matrix} \frac{kt^2(1 + e^{-kt})e^{-kt}}{(1 - e^{-kt})^3} - \frac{2te^{-kt}}{(1 - e^{-kt})^2} & 0 \\ 0 & 0 \end{matrix}$
5 Comparison of relative growth rates at each length	$g = \frac{(l_\infty - l)k}{l}$	$\begin{pmatrix} \frac{l_\infty}{l} - 1 \\ \frac{k}{l} \end{pmatrix}$	$\begin{pmatrix} 0 & \frac{1}{l} \\ \frac{1}{l} & 0 \end{pmatrix}$
6 Comparison of rates at which the asymptotic size is approached	$g = k$	$\begin{pmatrix} 1 \\ 0 \end{pmatrix}$	$\begin{pmatrix} 0 & 0 \\ 0 & 0 \end{pmatrix}$

tegrated squared difference over the specified range. For example, if $g_1 = \lambda_1 e^{-k_1 t}$ and $g_2 = \lambda_2 e^{-k_2 t}$, in which $\lambda_1 = k_2 l_{\infty 1}$ and $\lambda_2 = k_2 l_{\infty 2}$, we will rely on

$$D = \int_{t_{min}}^{t_{max}} (g_1(t) - g_2(t))dt.$$

The corresponding expectation and variance can also be approximated by the delta method.

We then apply each method to comparisons of the growth of males and females of two species of tiger prawn caught during tagging studies in northern Australia (Somers and Kirkwood 1991). We will consider two scenarios: 1) growth at age 0.5 yr (for methods 1, 2, and 4) or growth at length 30 mm (for methods 3 and 5); 2) growth at age one yr (for methods1, 2, and 4) or growth at length 35 mm (for methods 3 and 5). In order to verify that our test assumption that D was normally distributed, we obtained frequency plots for the bootstrapped estimates of the growth parameters.

Results

We first bootstrapped the parameter estimates for each group to assess whether our assumption that the parameters were normally distributed was valid. The plot for male *P. semisulcatus* showed that there was little evidence of skewness in our estimates (Fig. 2). Plots for other groups are similar and not shown here. The t tests proposed in this paper, although based on normal distributions, are well known to be robust to violation to normality (which is why they are also known as "robust" test in statistics). On the other hand, the proposed tests rely only on mean and covariance estimates and the covariance matrix is often obtained from asymptotic distribution (normal) of the estimates in nonlinear regression.

We tested for the overall significance of each comparison before proceeding with testing the six methods. All were highly significant ($P<<0.00001$) and T^2 statistics ranged from 43.2 for the comparison of *P. semisulcatus* females versus *P. esculentus* females to 385.7 for *P. esculentus* males versus *P. semisulcatus* females. Given that the overall growth curves differed among species, then it is reasonable to then look further at the growth rates yielded by the different methods.

The growth models for the six methods of comparing growth and their first and second derivatives differed between methods (Table 1). The growth parameters used in the comparison show apparent differences in the size of both l_∞ and k among the species and sexes (Wang, 1998). These differences in the absolute value of each parameter translate into quite large differences in the shape of the growth curves (Fig. 1). The effect is most striking for *Penaeus semisulcatus*, but does growth differ? Is it affected if we choose a particular length or age?

The results of tests from the six methods are shown in Table 2. The difference in lengths between P. *esculentus* and P. *semisulcatus* at the age of 0.5 yr is not significant for either males or females (in method 1 in Table 2), but the difference becomes very significant at age 1 yr. This result is consistent with the plot in Figure 1. However, the conclusion is reversed when comparing growth rate (method 2 in Table 2) instead of length. The relative growth rates at either age (0.5 yr or 1 yr) for *P. esculentus* do not differ significantly between males and females (method 4), whereas the rates at length 30 mm or 35 mm differ significantly. This is also biologically plausible because the growth rate at length 35 mm is very close to zero for *P. esculentus* males (the asymptotic size is only 35.6 mm) and there is a substantial growth to be gained for females (the asymptotical size is 44.7 mm). For method 6, the comparion is independent of specified length or age (two scenarios give the same results).

In prawn farms, *P. esculentus* and *P. semisulcatus* are harvested after 6 or 12 months, depending on the circumstances, such as the farmer's need to increase the number of generations within the growing season at higher latitudes. Tests comparing the growth of each sex of each species (Table 3) show that the significance of the results varies with the hypothesis being tested. For example, the comparison of length-at-age (method 1) of *Penaeus semisulcatus* and *P. esculentus* and females was not significant ($P<0.87$) at both six months of age (Table 3). However, when the absolute growth rates of the two species were compared (method 2), they were highly significantly different ($P<0.001$). Other tests, such as comparisons of the growth of male and female *P. semisulcatus*, were highly significant for all methods ($P<0.001$). As Francis (1996) pointed out, the results from all comparisons with methods 3 and 5 produce similar results and methods 4 and 6 give very similar results but in the opposite direction.

Table 2

The von Bertalanffy growth parameter estimates of *Penaeus esculentus* and *P. semisulcatus* from the Gulf of Carpentaria, northern Australia, used in growth comparisons between sexes of each species and between the two species for the same sex. The unbiased estimates were obtained by the equation of Wang (1998) and based on tagged prawn data from Somers and Kirkwood (1991).

Species	Sex	n	$l_\infty \pm$ SE (mm)	$k \pm$ SE (per yr)	Cov (l_∞, k)
P. esculentus	M	333	35.6 ± 0.3	2.8 ± 0.2	−0.0565
	F	224	44.7 ± 1.2	2.6 ± 0.3	−0.395
P. semisulcatus	M	159	38.6 ± 0.5	2.6 ± 0.2	−0.0886
	F	204	54.9 ± 1.7	1.8 ± 0.2	−0.2788

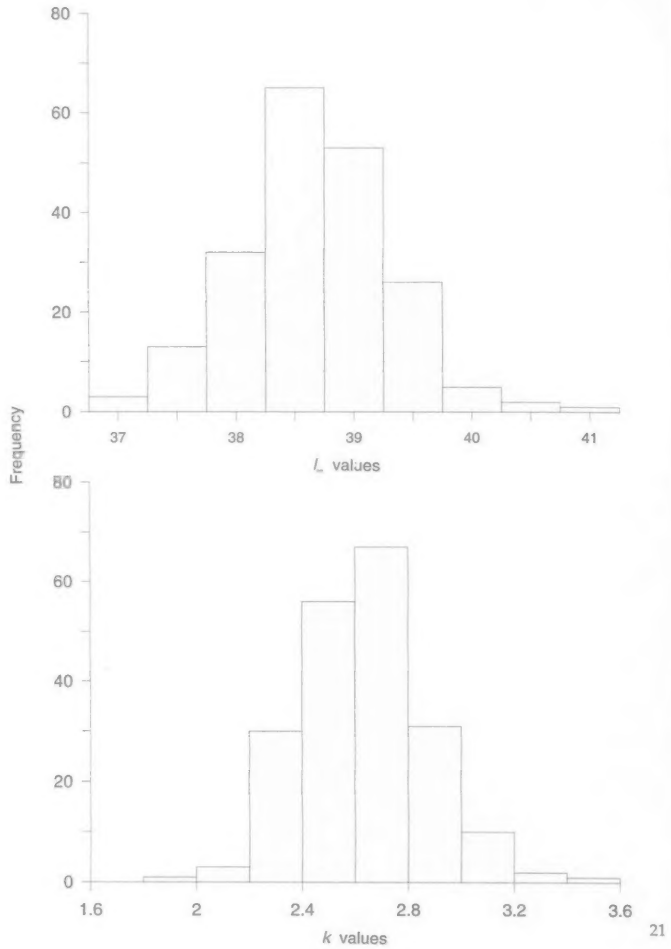

Figure 2

Plots of the frequency histogram of 200 bootstrapped estimates of l_∞ and k for *P. semisulcatus* males.

Our tests, in which the two tiger prawn species were compared, show that the significance of the results varies with the hypothesis. In our example, we have tried to choose lengths and ages that were approximately comparable. The results of the six tests for any particular interspecific or intraspecific hypothesis under either scenario are not directly comparable because methods 1, 2, and 4 compare growth rate at age (6 month or 1 yr) and the other methods compare growth rate in relation to length (30 mm or 35 mm). This distinction is more important for the interspecific comparisons because growth rate, rather than sexes, is more likely to vary between species for most phyla.

Discussion

Tests to compare growth by comparing length-at-age (method 1) show that there were no significant differences in the size of each sex of the two species, but there were highly significant differences in size between the sexes of each species. This finding differs from the interpretation if k-values were compared (method 6). In the situation where a farmer is deciding which species reaches a minimum marketable size earlier, we think that method 1 would be the most logical to use. However, if the farmer were trying to decide the potential benefit or tradeoff of

Table 3

Results of tests to compare within-species and between-species differences in the growth of males (M) and females (F) of two commercial penaeid prawns, *Penaeus esculentus* (*P.e*) and *P. semisulcatus* (*P.s*), from the Gulf of Carpentaria, northern Australia. The unbiased estimates from tagged prawns were obtained by the equation of Wang (1998). $D = g(\hat{\beta}_1) - g(\hat{\beta}_2)$, V = the corresponding variance. Comparisons were made against the alternate hypothesis $g(\beta_1) \leq g(\beta_2)$ under two scenarios: 1) at age (t) = 0.5 yr for methods 1, 2, and 4 or at length (l) = 30 mm for methods 3 and 5; 2) at age (t) = 1 yr for methods 1, 2, and 4 or length (l) = 35 mm for methods 3 and 5. P_1 and P_2 are the P-values under scenarios 1 and 2.

			Scenario 1 (l=30 mm or t=0.5 yr)			Scenario 2 (l=35 mm or t=1.0 yr)		
Method	Comparison	Type of comparison	D	V	p_1	D	V	p_2
1 Comparison of lengths at each age	*P.s* M vs. *P.s* F	within-species	–4.0	1.2	0.001	–9.7	0.4	0.001
	P.e M vs. *P.e* F	within–species	5.6	1.5	0.001	7.9	0.3	0.001
	P.e M vs. *P.s* M	between-species	1.3	1.0	0.18	2.4	0.3	0.001
	P.e F vs. *P.s* F	between-species	–0.26	1.7	0.87	4.2	0.4	0.001
2 Comparison of absolute growth rates at each age	*P.s* M vs. *P.s* F	within-species	–12.7	1.2	0.001	–9.2	2.0	0.001
	P.e M vs. *P.e* F	within-species	7.2	2.2	0.001	2.7	2.2	0.23
	P.e M vs. *P.s* M	between-species	2.8	1.3	0.03	1.4	1.3	0.29
	P.e F vs. *P.s* F	between-species	8.3	2.2	0.001	7.9	2.7	0.003
3 Comparison of absolute growth rates at each length	*P.s* M vs. *P.s* F	within-species	–21.4	1.6	0.001	–25.6	0.94	0.000
	P.e M vs. *P.e* F	within-species	22.3	2.3	0.001	23.4	1.08	0.000
	P.e M vs. *P.s* M	between-species	6.9	0.8	0.001	7.9	0.94	0.000
	P.s F vs. *P.e* F	between-species	5.9	2.7	0.03	10.03	1.09	0.000
4 Comparison of relative growth rates at each age	*P.s* M vs. *P.s* F	within-species	–0.27	0.08	0.001	–0.16	0.05	0.001
	P.e M vs. *P.e* F	within-species	0.06	0.11	0.59	0.03	0.06	0.60
	P.e M vs. *P.s* M	between-species	0.06	0.08	0.49	0.03	0.04	0.49
	P.s F vs. *P.e* F	between-species	0.27	0.12	0.03	0.15	0.06	0.02
5 Comparison of relative growth rates at each length	*P.s* M vs. *P.s* F	within-species	–0.71	0.05	0.001	–0.73	0.03	0.000
	P.e M vs. *P.e* F	within-species	0.74	0.08	0.001	0.67	0.03	0.000
	P.e M vs. *P.s* M	between-species	0.23	0.03	0.001	0.22	0.03	0.000
	P.s F vs. *P.e* F	between-species	0.20	0.09	0.03	0.29	0.03	0.000
6 Comparison of rates at which the asymptotic size is approached	*P.s* M vs. *P.s* F	within-species	0.84	0.26	0.001	0.84	0.26	0.001
	P.e M vs. *P.e* F	within-species	–0.22	0.4	0.58	–0.22	0.4	0.58
	P.e M vs. *P.s* M	between-species	–0.20	0.28	0.49	–0.20	0.28	0.49
	P.s F vs. *P.e* F	between-species	–0.82	0.39	0.03	–0.82	0.39	0.03

leaving the prawns in the ponds for longer, then one of the methods that test for relative changes in growth rate (method 4 or 5) would probably be more appropriate.

The difference in parameter estimates, and hence growth rates, may have important implications when researchers are trying to compare growth between species or between regions. Francis (1988) argued that length-at-age data do not contain precise information on the expected growth rate of fish of a given length. He concluded that length-at-age data and tagging data contain different information on growth; therefore the parameters estimated from them had different meanings and were not directly comparable.

Our proposed tests for different methods, including the overall test, aim to incorporate all the parameters and the overall uncertainties and correlations between each other. Further research can be carried out to study the robustness of the proposed test and to apply it to other growth models. The method suggested for constructing tests to compare growth rates could be easily modified to apply to other types of growth equation besides the von Bertalanffy equation.

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Occurrence of Pacific sardine, *Sardinops sagax*, off southeastern Alaska

Bruce L. Wing
James M. Murphy
Thomas L. Rutecki

Auke Bay Laboratory
Alaska Fisheries Science Center
11305 Glacier Highway
Juneau, Alaska 99801-8626
E-mail address (for B. Wing): Bruce.Wing@noaa.gov

Pacific sardines, *Sardinops sagax* (Jenyns, 1842), are an important forage and commercial species off central and southern California. From the late 1920s through the early 1940s, sardines were a major resource of the oil and meal fisheries of British Columbia, Washington, and Oregon (Hart, 1973). In 1931, sardines were unusually abundant on southern and central British Columbia fishing grounds and more numerous than usual in northern British Columbia (Shultz et al., 1932). In the early 1940s, however, yield of these fisheries declined radically and the species range was restricted to waters off central and southern California. After the decline, Pacific sardines were rarely reported north of the California–Oregon border (Reid, 1960; Mearns, 1988). Since 1992, Pacific sardines have again been observed off southern and central British Columbia (Hargreaves et al., 1994; McFarlane and Beamish, 1999).

Although the occurrence and changes in abundance of Pacific sardines in British Columbia waters are well documented, the presence of this species off Alaska is poorly documented. Schultz et al. (1932) reported Pacific sardines from Alaska on the basis of 24 adult specimens collected 8 August 1931 from the Cape Ommaney herring fishery (Clark, 1936; 1947). No additional specimen was documented from Alaska until 1992, when larval Pacific sardines were collected southwest of the Shumagin Islands, southwestern Alaska (Busby et al[1]).

Specimen collection

Eight adult sardines were captured in a surface trawl at 57°31′N, 136°34′W, 28 km west of Khaz Point, northern southeastern Alaska, on 20 August 1998. The fish were captured during a National Marine Fisheries Service research cruise to compare rope trawl and gill-net sampling methods for juvenile sablefish, *Anoplopoma fimbria*, and juvenile salmon, *Oncorhynchus* spp., in coastal Alaska. We used a Nordic 264-rope trawl (24-m horizontal opening, 30-m vertical opening) equipped with 3-m foam-filled doors and extra trawl floats to hold it at the surface.

Two additional specimens from Garnet Point (54°43′N, 130°41′W), near Nakat Bay, southern southeastern Alaska, were taken in a commercial salmon gill net on 1 September 1998. Fishermen reported that sardines were common but not numerous in eastern Dixon Entrance near Nakat Bay through August and early September 1998.

Both collections were frozen before being transported to the Auke Bay Laboratory, where lengths and weights of thawed fish were recorded. The fish were fixed in 4% formaldehyde, transferred to isopropyl alcohol, and then dissected to determine sex, maturity, and stomach contents. The fish were then deposited in the Auke Bay Laboratory reference collections.

Results

The 10 Pacific sardines averaged 233.3 ±11.30 mm standard length and 183 ±38.02 g wet weight (Table 1). On the basis of scale annuli, the collections were divided equally between 7- and 8-year-old fish. They were equally divided between males and females, and all gonads were in the resting stage. The fish had been feeding and had mesenteric fat deposits. Identifiable foods consisted of diatoms and euphausiids (*Euphausia pacifica* and *Thysanoessa* spp.) at Garnet Point and euphausiids (*E. pacifica* and *Thysanoessa* spp.) and small calanoid copepods (*Acartia* spp. and *Pseudocalanus* spp.) at Khaz Point.

Discussion

The occurrence of adult Pacific sardines in Alaska coastal waters is probably due to a northward extension of their summer feeding migration. Pacific sardines have a complex migration and spawning cycle, moving northward from California spawning areas during summer. The largest, oldest fish reach central Vancouver Island or farther north (Hart 1973). Historically, few Pacific sardines have overwintered in southern British Columbia (Schultz et al., 1932; Hart, 1943; Hargreaves et al., 1994), but during February–April 1998, juvenile sardines were observed off the western coast of Vancouver (McFarlane and Beamish, 1999). Sardines overwintering in British Columbia could migrate north into Alaska waters the following summer. In summer 1931, sardines were observed at many northern British Columbia locations near the Alaska border and were common in the fall and winter

[1] Busby, M. S., W. W. Watson, and W. Shaw. 2000. Identification of larval and juvenile Pacific herring (*Clupea pallasi*) and Pacific sardine (*Sardinops sagax*) and their distribution in waters off British Columbia and in the Gulf of Alaska. *In* prep. [Available from M. S. Busby, RACE, Alaska Fisheries Science Center, 7600 Sand Point Way NE, Bin 15700, Seattle WA 98115-0070.]

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Table 1

Biological data for Pacific sardines, *Sardinops sagax*, collected in Alaska, during summer 1998.

Standard length (mm)	Wet weight (g)	Age (yr)	Sex	Maturation stage	Food
Collection no. AB 98-39, Garnet Point, 54°43′N, 140°41′W, 1 Sep 1998, 2 specimens					
233	153	7	M	resting	diatoms
235	155	7	M	resting	diatoms and euphausiids
Collection no. AB 98-44, Khaz Point, 57°31′N, 136°34′W, 20 Aug 1998, 8 specimens					
225	155	7	M	resting	euphausiids and copepods
225	157	8	M	resting	trace of zooplankton
230	204	8	F	resting	trace of zooplankton
215	156	7	F	resting	trace of zooplankton
255	254	8	F	resting	euphausiids and copepods
240	207	8	F	resting	trace of zooplankton
230	157	7	F	resting	trace of zooplankton
245	232	8	M	resting	euphausiids and copepods

herring fisheries of southern British Columbia (Shultz et al., 1932).

Both years in which Pacific sardines were observed in southeastern Alaska were exceptionally warm and at the end of strong El Niño periods. The occurrence of sardines in Alaska reported in our study followed the exceptionally strong 1997–98 El Niño and is similar to the 1931 occurrence of Pacific sardines in Alaska, which followed the 1930–31 El Niño. Increased water temperature associated with El Niño events typically results in northward range extensions and anomalous distributions of fishes (Radovich, 1961; Schoener and Fluharty, 1985; Mearns, 1988). Although not specifically associated with sardines, several fishes were recorded north of their normal ranges during the 1930–31 (Walford, 1931; Mearns, 1988), 1982–83, and 1997–98 El Niños (Table 2). Included in 1997–98 records is an unconfirmed report of coho salmon, *Oncorhynchus kisutch*, feeding on northern anchovy, *Engraulis mordax*, near Yakutat, Alaska. Northern anchovy previously have not been reported north of the Queen Charlotte Islands, British Columbia. Interannual variations of El Niños and their effects on the distribution of marine organisms are difficult to assess because adequate time series data are lacking (Schoener and Fluharty, 1985), especially for Alaska coastal waters before 1960. In addition, not all unusual occurrences associated with El Niños are range extensions. More frequently, these occurrences are the result of anomalous strayings beyond normal ranges or are the result of changes in abundance or shifts in habitats (Table 2).

Although water temperature is a factor determining sardine distribution (Radovich, 1961), other factors may determine abundance and whether a range extension persists. Most Pacific sardine spawning occurs off southern California at 15–18°C temperatures (at a lower threshold limit

Table 2

Inter-El Niño comparison of unusual northern occurrences of marine fishes in Alaska coastal waters. Occurrences were coded according to Schoener and Fluharty (1985). E = range extension, H = habitat anomaly, A = range anomaly, C = change in abundance (+ or –). Sources: 1930–31 (Shultz et al., 1932); 1957–58 (Radovich, 1961); 1982–83 (Karinen et al., 1985; Pearcy and Schoener, 1987); 1991–94 (Wing, unpublished files); 1997–98 (Wing, unpubl. files).

Species	1930–31	1957–58	1982–83	1991–94	1997–98
Sardinops sagax	E				E
Alosa sapidissima			A	A	
Engraulis mordax					E
Cololabis saira			A		A
Sarda chiliensis		E	A		
Scomber japonicus				C+	C+
Thunnus alalunga		C+	C+		C+
Thunnus thynnus		E			
Seriola lalandi					E
Trachurus symmetricus				C+	C+
Merluccius productus					C+
Sphyraena argentea		A	A		A
Mola mola			A	A	A
Brama japonica			A	C+	C+
Atractoscion nobilis		E			
Balistes polylepis			E		
Prionace glauca			A/C+		C+
Carcharodon carcharias			A		A

of 13°C) (Ahlstrom, 1954). Laboratory studies have shown high mortalities and abnormal development at temperatures below 14°C (Lasker, 1964). There is some spawning off northern Oregon (Clark, 1938; Ahlstrom, 1948; Bentley et al., 1996). No spawning has been documented off British Columbia, although mature females with loose eggs have been reported from British Columbia (Walford and Mosher, 1941; Hart, 1943, 1973). Water temperatures off the northern British Columbia and southeastern Alaska coasts are sufficiently high for successful spawning and development of eggs and larvae in July and August. The progeny may not survive, however, to maturity if subsequent foraging, predation, and overwintering conditions are severe. If spawning does occur off British Columbia, it may be only a temporary extension of the spawning range and may not create long-lasting populations. In Alaska, such a temporary range extension was observed in the early 1980s for the California market squid, *Loligo opalescens*, whose range expanded northward for several years before contracting southward again (Wing and Mercer, 1990).

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Announcement

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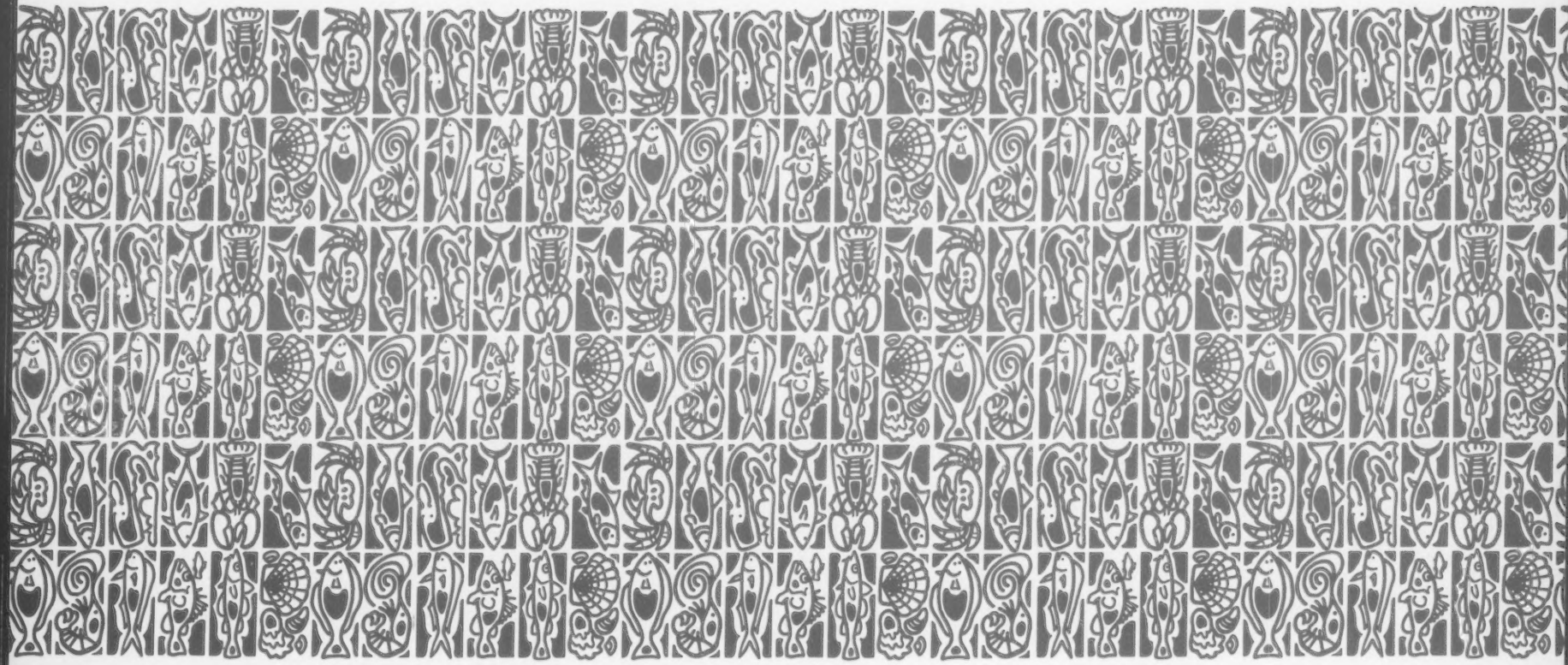

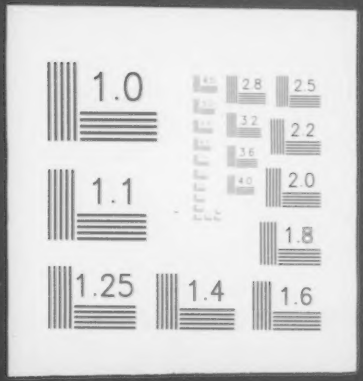
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